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Benthic consumers and autotrophs in recovering acidified lakes: patterns and processes

by

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ABSTRACT

The relative importance of grazing and abiotic factors to benthic autotrophs was examined in six recovering acidified boreal lakes. Chemical variables (pH, DOC, phosphorus) were significant predictors of biomass and taxonomic composition of autotrophs and consumers. A nonsignificant relationship between autotrophic and consumer biomass, and stable isotopic evidence of detrital and planktonic food sources, suggested grazing pressure was weak. A 2-factor (stress x consumer size) experiment tested if grazing pressure was maintained across three acid-stressed and recovered lakes owing to a compensatory grazer size shift. Abiotic stress suppressed autotrophic biomass and altered community composition. Consumers did not affect autotrophic biomass, but large grazers influenced composition in recovered lakes. Differential impacts of consumers and abiotic stress on autotrophic communities highlighted their capacity to compensate for weak natural disturbances (e.g., grazing), but not chronic stress (e.g., anthropogenic acidification). The primacy of abiotic factors in structuring benthic communities suggested biological recovery remained incomplete.

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LIST OF KEY TERMS AND ABBREVIATIONS

Consumers – collectively, all functional feeding groups (consumers = predators + grazers + omnivores)

CPOM - coarse particulate organic matter

DIC – dissolved inorganic carbon

DOC – dissolved organic carbon

fga – filamentous green algae

FPOM – fine particulate organic matter

Recovery – the re-establishment of abiotic and biotic factors that approximate unperturbed reference conditions (e.g., long-term reference lakes, Experimental Lakes Area, Canada)

Stress – an environmental variable (e.g., pH) that exceeds its natural range of variation, which results in an adverse effect on species within a community

TDP – total dissolved phosphorus

TN – total nitrogen

CHAPTER ONE

GENERAL INTRODUCTION

Abiotic and biotic regulation of biological recovery

Widespread chemical recovery in anthropogenically acidified lakes followed reductions in sulphur emissions from industrial activity (Hutchinson and Havas 1986; Keller and Pitblado 1986; Driscoll et al. 2001), but biological recovery responses to these improvements in water quality remain unclear. Studies suggest that simple reversal of stress trajectories seldom occur and that recovery responses are delayed, inconsistent, or not occurring at all (Frost et al. 1998; Snucins et al. 2001; Vinebrooke et al. 2003a). Limited evidence shows that the return and re-establishment of viable populations (i.e., biological recovery) of benthic autotrophs, termed periphyton, are delayed behind chemical improvements (Dixit et al. 1992; Vinebrooke and Graham 1997; Findlay et al. 1999). This is unexpected, as species with high fecundity and dispersal abilities, specifically biota at lower trophic levels, are expected to readily re-colonize recovering acidified lakes (Schindler 1987a; Yan et al. 1995).

The ecological effects of delayed periphyton recovery are not known. It is anticipated that delayed recovery, particularly in species-poor boreal ecosystems where only a few species perform ecosystem processes, may have considerable negative impacts on whole-lake energetics and ecosystem stability when subjected to other global

stressors (e.g., climate warming). Disruption of periphyton communities can influence the rest of the aquatic food web by potentially altering food availability and habitat refugia for benthic invertebrates and fish (Turner et al. 1995; Lowe and Pan 1996).

Recovery by algae is regulated by abiotic and biotic factors (Vinebrooke 1996; Graham and Vinebrooke 1998). Early studies of algal recovery in acidified lakes suggested that abiotic factors primarily regulated overall recovery rates, but not lag responses to chemical changes (Dixit et al. 1992; Nicholls et al. 1992; Vinebrooke 1996; Vinebrooke and Graham 1997). Species recruitment models suggest dispersal limitation and biotic exclusion are mechanisms for delays in recovery responses (e.g., Yan et al. 2003). In general, recovery trajectories are influenced by four factors: the extent of chemical recovery, availability of colonists, mechanisms for overcoming dispersal barriers imposed by distance or lack of connectivity, and biotic interactions (Keller and Yan 1998; Yan et al. 2003).

Chemical recovery in acidified lakes is quantified by increases in pH and alkalinity coupled with reductions in sulphate, base cations, and metals (Snucins et al. 2001; Keller et al. 2003). The extent of chemical recovery varies among lakes, owing to differences in bedrock geology and lake water residence time that have implications for the biota (Keller et al. 1999; Snucins et al. 2001). Chemical recovery proceeds more quickly in lakes underlain by granite or limestone that provide increased mineral

weathering relative to lakes found on erosion-resistant orthoquartzite bedrock, which has a lower buffering capacity against acidic precipitation (Gunn et al. 2001; Snucins et al. 2001). Shorter lake water residence times result in increased flushing rates of sulphate inputs, such that lakes can re-establish conditions typical of circumneutral lakes, whereas long water residence times can impede chemical recovery (Schindler 1987b; Jefferies et al. 2003).

Algal communities are highly responsive to chemical changes in water quality (e.g., Turner et al. 1987, Vinebrooke 1996). Decreased acidity signifies an important improvement in environmental suitability, with pH 6 recognized as a critical threshold for supporting acid-sensitive taxa (Schindler 1988; Keller et al. 1990; Havens et al. 1993). For example, noticeable declines in filamentous green algae (fga) that proliferated in littoral zones of acidified lakes, have been observed as chemical recovery proceeds above pH 6 (Turner et al. 1995). The dominance of fga was attributed to a physiological tolerance for low acidity and a superior ability to compete for reduced levels of available dissolved inorganic carbon (DIC) associated with acidification (Turner et al. 1987; Planas et al. 1996). Furthermore, abiotic factors (e.g., DIC, DOC) are key determinants of the structure and composition of periphyton communities in boreal lakes in the early stages of recovery from severe acidification (Vinebrooke 1996; Vinebrooke and Graham 1997).

Following re-establishment of a suitable chemical environment, sensitive species lost to acidification are expected to return and re-colonize. Under favorable environmental conditions, algae are not expected to be dispersal limited because of immigration from nearby waterbodies (Finlay and Clark 1999; Finlay 2002) and rapid recruitment from sedimentary resting structures (Hansson 1996), which serve as potentially species-rich inoculums. Following pH increases in an experimentally acidified lake (L302S, Experimental Lakes Area, Canada), Findlay (2003) found immigration of pelagic algae (i.e., phytoplankton) from local lakes coupled with in-lake sources quickly shifted the phytoplankton community towards those characteristic of circumneutral lakes. Vinebrooke (1996) also demonstrated experimentally that algal re-colonization in recovering acidified lakes is not impeded by dispersal barriers (e.g., physical distance, topographical barriers) that may limit other invertebrates and fish (Gunn and Keller 1990; Keller and Yan 1998; Mills et al. 2002; Snucins et al. 2001).

Biotic interactions become increasingly influential on recovery trajectories as chemical recovery proceeds (Vinebrooke 1996; Yan et al. 2004), owing to the re-establishment of higher trophic levels eliminated by stress. Delays of several years in algal response to chemical improvements observed in chronically acid-stressed lakes (Arnott et al. 2001; Vinebrooke et al. 2003a) may be attributable to biotic exclusion by persistent, acid-tolerant consumers. The structure and composition of

higher trophic levels modified by acidification, which altered predation, grazing, and competition regimes, could persist during recovery, thereby suppressing algal recovery. For example, the loss of an acid-sensitive, visually oriented predator (e.g., lake trout) reduced predation pressure on acid-tolerant predatory invertebrates (e.g., corixids, notonectids, and odonates) in fishless acidified or recovering acidified lakes (Keller et al. 1992; Bendell and McNicol 1995). This shift toward intense predation by large populations of predatory invertebrates can impede or prevent the establishment of prey, such as smaller algivorous invertebrates (Eriksson et al. 1980; Carbone et al. 1998; Keller et al. 1999). In recovering acidified lakes, if physical barriers prolong the return of fish and large invertebrates (that lack an aerial stage), acid-tolerant invertebrates will persist (Keller et al. 1992; Vinebrooke et al. 2003b) and may delay or completely restrict the colonization of returning invertebrates and algae despite suitable environmental conditions (Frost et al. 1998; Holt and Yan 2003; Vinebrooke et al. 2003a).

Conventionally, grazing pressure in benthic environments has been assumed to decline during acidification (Schindler 1987a) owing to declines in many acid-sensitive grazer groups, such as larval insects, amphipods, snails, and fish (Hesthagen et al. 1996; Carbone et al. 1998; Mills et al. 2002). A typical community response to stress is a size shift towards smaller-bodied consumers that accompanies the loss of acid-sensitive species (Odum 1985; Rapport et al. 1986; Bendell and McNicol

1987). This event may have implications for size-selective feeding on periphyton (Tate and Hershey 2003). The hypothesized decline in grazing with acidification leads to an expected increase in grazing with recovery as acid-sensitive grazers re-establish due to suitable environmental conditions. However, a number of species in these groups lack active dispersal abilities and may not readily re-colonize acidified lakes. This leads to a biological delay response in trophic levels which may have top-down effects on periphyton. In addition, it is possible that if acid-sensitive grazers do not re-establish during chemical recovery, then extensive mats of filamentous green algae (fga) might suppress other periphytic species. Evidence of competitive exclusion by acid-tolerant species provided by Findlay et al. (1999) showed that as lake pH increased during recovery, robust acid-tolerant phytoplankton (e.g., dinoflagellates) prevented the re-establishment of pre-stress communities by restricting the return of dominant chrysophytes. Therefore, biological recovery may be limited by the re-establishment of biotic interactions of typical of pre-stress ecosystems (Keller and Yan 1998). Currently, there is a lack of empirical evidence demonstrating the relative importance of biotic interactions as chemical recovery proceeds in acidified lakes.

Species-level responses and compensatory dynamics

Biological recovery is best recognized by species-level responses, owing to species-specific differences in physiological tolerances and

processes (e.g., dispersal) associated with recovery from stress (Nicholls et al. 1992; Vinebrooke 1996; Vinebrooke and Graham 1997; Findlay et al. 1999; Yan et al. 2003). Similarly, species responses to environmental stress are typically more prevalent and occur earlier than community-level responses (Schindler et al. 1985; Strecker et al. 2004), supporting Odum's (1985) predictions of ecosystem response to stress. Species-level size reductions, both as morphological changes within a taxa (e.g., *Achnanthes minutissima*; Cattaeno et al. 1998) and taxonomic shifts within a community (e.g., benthic macroinvertebrates; Bendell and McNicol 1987), also occur in response to stress and are expected to increase with recovery. Compensatory shifts in the species composition of communities often maintain community-level properties (e.g., primary production, herbivory) despite abiotic environmental disturbances or changes in biotic interactions (Schindler 1987; Frost et al. 1995; Tilman 1996; Vinebrooke et al. 2003b). Ernest and Brown (2001) suggest this is because individual species abundances are regulated by a greater number of environmental variables (e.g., competition, dispersal, abiotic conditions, pathogens, etc.) than rates of community-level processes, such as primary production, which are affected primarily by light.

Compensatory dynamics involve the replacement of a species that declined in response to an environmental stress, with a tolerant species that performs a similar ecosystem function (e.g., primary production; Klug et al. 2000; Vinebrooke et al. 2003b). Species-specific sensitivity to

stress, competitive interactions among species and vulnerability to predation have been identified as important mechanisms for compensatory dynamics (Ives 1995; Vinebrooke et al. 2003b). Compensation between species is expressed by negative covariances in population dynamics (Frost et al. 1995; Klug et al. 2000). Evidence of compensatory dynamics has been documented by phytoplankton in alpine ponds and boreal lakes (Vinebrooke et al. 2003b; Strecker et al. 2004), herbaceous vascular plants in grasslands (Tilman 1996; Wardle et al. 1999), zooplankton in freshwater lakes (Frost et al. 1995; Fischer et al. 2001), and rodents in a desert (Ernest and Brown 2001), emphasizing the generality of this ecological process.

Changes in environmental conditions (e.g., pH, temperature) can cause substantial changes in pelagic phytoplankton species composition and the abundance of certain species, creating an opportunity for compensatory dynamics by other species, without significantly altering overall production. During the experimental acidification of Lake 223 (Experimental Lakes Area, Canada), Schindler et al. (1985) reported the decline of many acid-sensitive chrysophytes, but primary production remained unchanged owing to increases in acid-tolerant chlorophytes and cyanophytes. Similarly, in response to warming and reduced grazing pressure, Strecker et al. (2004) found decreases in filamentous green algae were compensated for by increased abundances of phytoflagellates, which maintained total phytoplankton biomass.

The relative importance of compensatory species dynamics in recovering acidified lakes, which may maintain primary production within or grazing pressure on periphyton communities during recovery from acidification, is currently unknown. Research in aquatic ecosystems is primarily focused on pelagic communities (Vadeboncoeur et al. 2002), despite the importance of benthic periphyton to productivity and whole lake energetics (Hecky and Hesslein 1995; Vander Zanden and Vadeboncoeur 2002). Potentially different community responses to stress and recovery may arise between benthic and pelagic communities in anthropogenically acidified lakes, owing to a more variable physiochemical environment and complex biotic interactions in the benthic littoral zone.

Thesis objectives

The primary objective of this thesis was to identify the relative importance of abiotic and biotic mechanisms regulating the recovery of periphyton communities in acidified lakes. Differential species recovery trajectories and rates need to be quantified to model recovery and identify the necessity and appropriate timing of human intervention to facilitate recovery. This objective was met by using a survey approach to quantify the relationships between periphyton, benthic consumer communities and environmental conditions, and by experimentally testing the importance of size-selective grazing along a stress-recovery gradient in boreal lakes.

Chapter two is an investigation of the relationships between periphyton, benthic consumers, and environmental (i.e., water chemistry) conditions along a gradient of six recovering acidified boreal lakes in Killarney Park (Ontario, Canada). Survey results and ordination analyses were used to identify patterns between abiotic factors and benthic communities and to categorize benthic communities by size structure. In addition, stable isotope analyses were performed to confirm the primary carbon source and trophic structure of benthic consumers. With these results, testable hypotheses of the strength of biotic regulation on the abundance and taxonomic composition of benthic autotroph communities in recovering acidified lakes were generated.

Chapter three provides an examination of the role of size-selective grazing on periphyton communities as a regulatory mechanism in recovering acidified lakes. The results of an exclosure experiment that tested the hypothesis that grazing pressure is maintained between stressed and recovered lakes due to a compensatory size shift in grazer body size are presented. The influence of abiotic and biotic regulatory factors on the community structure and composition of periphyton is discussed.

Chapter four provides a summary of thesis findings, a synthesis of survey and experimental results, and proposes future research projects in recovering acidified lakes.

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CHAPTER 2

ENVIRONMENTAL PREDICTORS OF BENTHIC CONSUMERS AND AUTOTROPHIC COMMUNITIES ALONG A RECOVERY GRADIENT

Introduction

Abiotic and biotic factors affect ecosystem recovery from chemical stress (Yan et al. 2003). In particular, biotic factors expectedly supersede abiotic control of communities as species and trophic interactions become re-established during ecosystem recovery (Menge and Sutherland 1987). For example, grazing is expected to increasingly control benthic autotrophs (e.g., epilithic periphyton) as chemical conditions ameliorate during abiotic recovery from anthropogenic acidification as acid-sensitive grazers re-establish (Vinebrooke 1996; Vinebrooke et al. 2003a).

Many benthic consumers are capable of active aerial dispersal (e.g., aquatic insects), enabling them to track environmental changes in lakes (Jackson and Harvey 1993; Carbone et al. 1998; Bohonak and Jenkins 2003). In contrast, amphibians, fish, and invertebrates lacking aerial adult stages (e.g., amphipods, snails) exhibit delayed responses to chemical recovery, particularly in lakes that lack migratory routes connecting them to remnant populations in neighboring lakes (Jackson and Harvey 1993; Mills et al. 2000). However, recolonization by aquatic insects can also lag behind chemical recovery due to dispersal limitation or predation (Bendell and McNicol 1995; Carbone et al. 1998; Snucins

2003), thereby weakening relationships between benthic consumers, autotrophs, and the abiotic environment.

Autotrophic microbes are very responsive to environmental changes in lakes owing to their wide dispersal potential, fast growth rates, high fecundity, and emergence from sedimentary resting structures (Hansson 1996; Finlay 2002). For example, significant associations between benthic autotrophs and changes in acidity and dissolved organic carbon (DOC) occur during the early stages (pH < 6) of recovery from acidification (Vinebrooke et al. 2003a). However, autotrophic responses to abiotic improvements become variable within and between lakes at pH > 6 (Vinebrooke et al. 2003a). A potential explanation for such discrepancies is that these study lakes had different ecological histories, such that past environmental conditions alter future community responses (Fischer et al. 2001). Specifically, differences in recolonization by grazers could explain variation in autotrophic communities between lakes.

Ecosystem stress causes size-shifts in biological communities as smaller organisms are considered more stress-tolerant because of reduced energetic demands (Odum 1985; Cattaneo et al. 1998). In stressed lakes, size shifts are associated with changes in taxonomic and functional composition. Size reductions have been observed at the species- (Cattaneo et al. 1998) and community-level (Bendell and McNicol 1995). Conversely, a size shift towards larger sensitive species should occur during ecosystem recovery, but supporting evidence from

recovering stressed aquatic ecosystems is limited (but see Rask et al. 2001; Cattaneo et al. 2004).

The purpose of this study was to quantify relationships between environmental factors and the abundance and taxonomic composition of benthic consumers and autotrophs in six recovering acidified boreal lakes. My main objective was to test the hypothesis that biotic relationships between benthic consumers and autotrophic communities had become stronger than previously reported (Vinebrooke 1996; Vinebrooke and Graham 1997) as a result of an additional 10-yr period of ecosystem recovery in the study lakes. I expected that environmental variables would be better predictors of taxonomic changes rather than variation in aggregate properties (e.g., total biomass) because lower trophic levels exhibit greater compensatory capacities (Vinebrooke et al. 2003b). Also, I anticipated that benthic communities would show a size-shift towards larger taxa along the recovery gradient.

Methods

Study area

The survey lakes were located in Killarney Provincial Park (46°3'N, 81°21'W), southwest of Sudbury, Ontario, Canada (Fig. 2.1). The park contains approximately 600 lakes and is a 48,000 ha wilderness area that is protected from mining, forestry, or agricultural activities. Recalcitrant orthoquartzite bedrock underlies the acidic lake catchments, whereas the

circumneutral lakes are located in lowland areas with limestone, diabase, or sandstone bedrock with a higher buffering capacity (Snucins et al. 2001). Killarney Park was one of the first areas in Canada where the damaging effects of acidification were identified. As a result of spatial proximity to sulfide ore metal smelters in Sudbury and being located in an area of high deposition of long-range pollutants, the history of acidification in the region is well documented (e.g., Beamish and Harvey 1975; Dixit et al. 1992). Reduced industrial emissions of sulphur have lead to chemical and limited biological recovery in many lakes in the region (Keller et al. 1992; Snucins et al. 2001).

Survey lakes were selected based on pH, an abiotic determinant of lake recovery (Keller et al. 2003), such that lakes represented both acidified and recovered stages of a recovery gradient. The three acidified lakes chosen were Acid, Ruth-Roy, and Norway. The three pH-recovered lakes (i.e., lakes that acidified but have recovered to pre-acidification pH status) were A.Y. Jackson, Carlyle, and Little Sheguiandah (Vinebrooke and Graham 1997). The lakes functioned as independent samples because they were not physically connected to each other. Two of the acidified lakes (Acid and Ruth Roy) were fishless, while Norway Lake contained sparse populations of mudminnows (*Umbra limi*) and yellow perch (*Perca flavescens*)(Snucins and Gunn, Cooperative Freshwater Ecology Unit, Sudbury, Ontario, unpublished data). The three pH-recovered lakes contained yellow perch and smallmouth bass

(*Micropterus dolmieui*), along with brown bullheads (*Ictalurus nebulosus*) and pumpkinseeds (*Lepomis gibbosus*) in Carlyle and Little Sheguiandah.

Lake water chemistry

Water samples were collected monthly from the littoral study area within each lake for pH, conductivity, total nitrogen (TN), total dissolved phosphorus (TDP), dissolved organic carbon (DOC), and dissolved inorganic carbon (DIC) analysis. Lake pH was also measured using an Accumet AP61 portable pH meter (Fischer Scientific) on the collection date. Duplicate samples were analyzed at the Limnology Laboratory at the University of Alberta. In the lab, pH was measured on a Fisher Accumet model 925 meter and was compared to values recorded during summer sampling. Conductivity was measured using a Radiometer/Copenhagen model CDM83 meter. TN samples were predigested with alkaline potassium persulfate according to Ameel et al. (1993) and determined by flow injection analysis on a Technicon™ Autoanalyzer™. TDP was measured using standard colorimetric procedures following digestion with potassium persulfate (Menzel and Corwin 1965). DOC and DIC were both analyzed using a Shimadzu TOC-5000A analyzer with an ASI 5000A autosampler (Shimadzu Corporation, Kyoto, Japan).

Survey of benthic consumers

Zoobenthos in each lake were sampled monthly from June to August 2003. Samples from the shallow littoral (depth <1m) were collected using a D-frame kicksweep net (500-μm mesh size). To account for habitat heterogeneity, three time-standardized D-net sweeps were done in three different habitat areas for three minutes. Samples were pooled, stored in coolers, and sorted within six hours. Predatory consumers were separated from the samples until sorting.

All consumers were sorted taxonomically to family and then frozen until stable isotopic analyses could be performed. Invertebrates were examined under a dissecting microscope at 40x and 100x magnifications. Many invertebrates were collected as early instars and were difficult to identify to genus or species, therefore family level was used for all statistical analyses. All consumers were also measured for size at the widest part of the body (usually head or abdomen), and classified according to published dietary descriptions and functional feeding groups (Merritt and Cummings 1984; Thorp and Covich 2001). Of the 23 consumer families collected, nine were classified as grazers that feed primarily on algal, plant, or detrital material, nine were classified as omnivores, and five other families were classified as predators. After drying at 60°C for 96 h, samples were weighed. Dry weight for snails and

crayfish were shell-free. Samples were then prepared for stable isotope analyses.

Survey of benthic autotrophs

The survey was conducted monthly, on dates corresponding with zoobenthos collections, to characterize the autotrophic community on rocks (epilithic periphyton) in all six lakes. Five rocks were collected from the littoral area of each lake, and placed in a white porcelain tray. Periphyton was brushed from the upper surfaces of the rocks using a hard-bristled toothbrush, rinsed with filtered lake water and pooled together. The sampled surface area of the rocks was measured using foil wrap and recorded (Aloi 1990). Samples were visually inspected to remove large particulate contaminants or invertebrates. The harvested material was transferred from the tray to a 500-mL graduated cylinder and was filled to 200mL with filtered lake water. A 50-mL subsample was filtered and concentrated on Whatman GF/C glass microfiber filter papers and frozen for stable isotope analysis. A 100-mL subsample was preserved with Lugol's solution (Wetzel and Likens 2000) for taxonomic analysis. Samples were well mixed, large filaments were broken apart using surgical scissors, and diluted depending on the density of algal and detrital material before settling for one hour using the Utermöhl method (Wetzel and Likens 2000). Species lists were constructed for each sample by scanning the chamber, starting at a low magnification (200x) for

large colonies and filaments and then up to 400x and 1000x for all other taxa on a Leica DM-IRB inverted microscope. A minimum of 300 viable cells were identified and counted per sample, with cell viability based on chloroplast integrity for eukaryotic cells and pigmentation for cyanobacteria. Taxonomic identifications were made to genus level according to Prescott (1982) and Wehr and Sheath (2003). Duplicate counts of each sample were done and if species richness (i.e., number of species) varied by more than 20% between duplicates, a triplicate sample was counted.

Cell counts were converted to areal biovolumes using standard geometric formulae for shapes that approximate algal shapes (Hillebrand et al. 1999; Sun and Liu 2003). Biovolume is considered the most precise measure of algal abundance (Morin and Cattaneo 1992), and was estimated on a per-cell basis whether the cells were solitary or filamentous. A minimum of 20 cells per taxon was used to determine its mean dimensions when sufficient cell numbers were available. Calculations corrected for differences in sample surface area, enumeration area, magnification, cell size, density, and dilutions (Equation 2.1):

$$\text{Taxon areal abundance } (mm^3/m^2) = \frac{\#\text{ of algal units counted}}{\text{mL of sample surveyed}} * \text{dilution 1} * \frac{\text{mL of total sample}}{m^2 \text{ of tile scraped}} * \text{dilution 2} * \frac{mm^3}{\text{algal unit}}$$

(Equation 2.1)

Where:

mL of sample surveyed = surface area of counting cell * mL of sample settled,

dilution 1 = sample dilution factor prior to counting (10 or 40 times),

dilution 2 = dilution factor for mL of total sample taken (200 mL taken in field, 100 mL for taxonomic analyses)

Algal biovolumes were converted to biomass assuming a specific gravity of one.

Collection of detritus

Detrital material collected from D-net sweeps was used to characterize the near-shore particulate organic material (POM) in each lake. POM was filtered through a 150-µm sieve to separate coarse particulate organic material (CPOM) and fine particulate organic material (FPOM). FPOM was settled and filtered on to a Whatman GF/F glass microfiber filter (0.7-µm mesh size). All POM samples were visually inspected to remove large particulate contaminants or invertebrates. Duplicate samples were collected from each lake and frozen until stable isotope analysis.

Stable isotope analyses

Periphyton, POM, and benthic consumer samples (i.e., whole invertebrate, amphibian and fish tissue) were frozen, dried at 60°C for 48 h (periphyton and POM) and 72 h (consumers), and ground into a fine powder using a mortar and pestle. Dry samples were packed into 8 x 5mm tin capsules for isotopic analyses. Periphyton and POM samples were peeled from filter papers prior to packing. Isotope ratios are expressed in delta (δ) notation, defined as parts per thousand (‰) deviation from a standard reference material (Equation 2.2).

$$\delta X = (R_{sample} / R_{standard} - 1) * 1000 \qquad \text{(Equation 2.2)}$$

Where X represents $\delta^{15}N$ or $\delta^{13}C$ and R is the corresponding ratio of $^{15}N:^{14}N$ or $^{13}C:^{12}C$, respectively.

Stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope analyses were performed at the Environmental Quality Analysis Laboratory (Department of Biology, University of Regina, Saskatchewan, Canada). Dried samples of 1 - 2 mg were combusted using a NC2500 Elemental Analyzer (Thermoquest, CE Instruments) and introduced into a Finnigan MAT DeltaPlus mass spectrometer for gas isotope ratio measurements of $^{13}C/^{12}C$ and $^{15}N/^{14}N$. Standard materials were PeeDee belemnite (PDB) limestone for $\delta^{13}C$, and atmospheric nitrogen for $\delta^{15}N$. Two replicates of each sample were

measured. Experimental precision, based on the standard deviation of replicates of the internal standard, was 0.38 ‰ for $\delta^{15}N$ and 0.08‰ for $\delta^{13}C$. Insufficient material was available to perform time series analysis of stable isotopes. Therefore, periphyton, CPOM, FPOM samples and consumer samples (by family) were pooled to generate composite isotopic signals for each group within each lake type, providing estimates of variation across three acidified and three recovered lakes. Due to the minimal variation between isotopic baseline signals (~1 C unit and ~1 N unit) in the benthic food webs of each of the recovered and stressed lakes, data were combined to produce two figures which provide a more integrative illustration of the carbon flow and trophic structure, as well as a more powerful analysis (as a result of more organisms for some taxa). Aggregation of whole invertebrate or tissue samples eliminated individual variation in isotopic signature (Post 2002). To avoid a bias towards heavily sampled groups, when more than two $\delta^{15}N$ or $\delta^{13}C$ measurements per taxon were available in a lake, mean isotopic values were reported.

Statistical analyses

All data were normalized using natural $\log_{10}$-transformation prior to statistical analyses to stabilize variances and meet assumptions of homogeneity of variance. Multiple regression analyses using all environmental variables were conducted to identify significant, independent predictors of consumer and autotrophic biomass (Quinn and

Keough 2002). Criteria for inclusion in the multiple regression model was $P = 0.05$. Stepwise multiple regressions with backward selection were performed using SYTSTAT Version 10 (SPSS 2000). Repeated-measures analyses of variance (RM-ANOVAs) were used to evaluate the effects of chemical stress (i.e., acidity) on consumer and autotrophic biomass over the survey period (Scheiner and Gurevitch 2001). Data was checked for sphericity and if the assumption was violated, the *P*-value was adjusted using the more conservative Greenhouse-Giesser method. Repeated-measures multivariate analyses of variance (RM-MANOVAs) were used to test for differences in the functional composition of benthic consumer (Table 2.3) and autotrophic communities between stressed and recovered lakes. These analyses were completed using the general linear model (GLM) procedure in SYSTAT Version 10 (SPSS 2000). Variance ratios (VR), based on the variance of total consumer biomass related to the cumulative variance of the component functional group biomass, were used to quantify compensatory dynamics for consumer communities (Frost et al. 1995; Vinebrooke et al. 2003b). The variance of total biomass is equal to the sum of component taxa biomass plus their covariances. Compensatory dynamics existed when the variance ratio was less than one, signifying negative covariance between the taxa. Otherwise, if variance ratios were equal to or greater than one, then taxa varied independently or synchronously, respectively (Vinebrooke et al. 2003b).

All variance ratio testing was done on non-transformed data (Frost et al. 1995).

Canonical correspondence analysis (CCA; CANOCO 4.51, ter Braak and Smilauer 2003) was used to examine relationships among environmental variables and the taxonomic composition of both autotrophic and consumer communities. Log_{10}-transformations were done on all variables, including algal biovolume, consumer biomass, and water chemistry, with the exception of pH. This reduced the influence of large algal and consumer species and outliers that otherwise skew ordinations (ter Braak 1986). Data were screened prior to CCA to remove any ecologically irrelevant, redundant, and non-significant environmental variables (ter Braak 1987). Specifically, all CCAs were run using automatic forward selection. Biplot scaling was used to show the regression relations in CCA between species and species-derived sample scores and Monte Carlo permutation tests were applied (499 iterations) to establish the significance of eigenvalues. Species that did not occur in at least three samples were omitted from ordination analyses of autotrophic data.

Results

Lake water chemistry

The surveyed lakes varied (mean $\pm$ S.D) in pH (5.93 $\pm$ 0.74), conductivity (25.93 um/s $\pm$ 47.41), TN (277.79 µg/L $\pm$ 47.41), TDP (2.36

µg/L ± 1.56), DOC (2.97 mg/L ± 1.17), and DIC (1.04 mg/L ± 0.82). Chemical analyses confirmed that the six survey lakes could be grouped into stressed and recovered categories (Table 2.1). Acid-stressed lakes had an average pH of 5.4 that remained below the biologically critical threshold of pH 6 (Schindler 1988). Recovered lakes had a less acidic average pH of 6.42, along with higher concentrations of DIC, DOC and TDP. All lakes were oligotrophic, with TDP consistently higher in recovered lakes, especially in Little Sheguiandah Lake in May and June. TN and conductivity were comparable across study lakes during the survey.

Consumer community structure

TDP was the only significant predictor of consumer biomass, explaining 42.6% of the variation ($F_{2,14} = 5.19$, $P = 0.02$; Table 2.2). Total consumer biomass did not differ significantly between stressed and recovered lakes (Fig. 2.2a; RM-ANOVA, time x stress, $F_{3,12} = 0.61$, $P = 0.62$). Consumer ($R^2 = 0.02$, $P = 0.55$) and grazer ($R^2 = 0.05$, $P = 0.77$) biomass were not significantly correlated with periphyton biomass (Fig. 2.3).

Differences in the functional composition (i.e., traditional feeding groups) of consumer communities between stressed and recovered lakes were marginally significant (RM-MANOVA, time x stress, $F_{10,40} = 1.91$, $P = 0.07$)(Table 2.3; Fig. 2.2). Specifically, grazers were more abundant in recovered lakes (Fig. 2.2b), and omnivores were more common in

stressed lakes (Fig. 2.2c), while predators did not differ consistently between lakes (Fig. 2.2d). Consumer groups exhibited negative co-variances, resulting in variance ratios equaling less than one on day 30 (VR = 0.47), day 60 (VR = 0.45), and day 90 (VR = 0.44).

A greater proportion of total consumer biomass consisted of large-bodied consumers in recovered relative to stressed lakes (Fig. 2.4a). In particular, large (> 10 mm maximum body width) consumers were present only in the recovered lakes. Small-bodied consumers were more common in stressed lakes, with the majority of consumers less than 2.5mm wide (Fig. 2.4a). A shift from small to large grazers was evident between stressed to recovered lakes (Fig. 2.4b). A similar pattern was evident for omnivores (Fig. 2.4c). In both lake types, predators made the greatest contribution to total biomass in the 2.5-10mm size class (Fig. 2.4d).

The taxonomic composition of consumer communities differed between stressed and recovered lakes. Of the 23 observed families, seven were absent from the stressed lakes and two were missing from the recovered lakes (Table 2.2). Corixids, chironomids, and odonates characterized consumer communities in stressed lakes and ephemeropterans, tadpoles, and minnows in recovered lake communities.

CCA captured 34.5% of the total variance in consumer species data with four axes. The first axis significantly ($F = 2.31$, $P = 0.05$) explained 15.5% of the species variance, and was best described by DOC ($r = 0.96$) and pH ($r = 0.81$) (Fig. 2.5). In particular, ranids (i.e., tadpoles;

No. 3) and cyprinids (No. 7), and to a lesser degree viviparids (No. 11), gammarids (No. 2), and ephemeropterans (No. 10) were more abundant in coloured (i.e., higher DOC) circumneutral lakes. In contrast, corixids (No. 12) and gyrinids (No. 6) were more dominant in more clear, acidic lakes.

CCA axis 2 was most strongly correlated with autotrophic biomass (r = -0.54) and conductivity (r = 0.62) (Fig. 2.5). Herbivorous ranids (No. 3) and cyprinids (No. 7) were positively associated with the periphyton biomass vector. Gammarids (No. 2) and ephemeropterans (No. 10) inhabiting more chemically concentrated circumneutral lakes were separated along the conductivity axis from corixids (No. 12) in more dilute, acidic lakes.

Stable isotope signatures

Inferred primary carbon sources of consumers differed between stressed and recovered lakes (Fig. 2.6). In stressed lakes, many consumer $\delta^{13}C$ values were more closely aligned with detrital (CPOM, FPOM) signals than with periphyton, except for Asellidae and Cambaridae (Fig. 2.6a). In contrast, a greater proportion of consumers (cambarids, limnephilids, corydalids, viviparids) paralleled periphyton $\delta^{13}C$ ratios in the recovered lakes (Fig. 2.6b). Many consumers, including chironomids, dytiscids, gomphids, and notonectids in stressed lakes and gomphids,

odonates, and asellids in recovered lakes, had more negative $\delta^{13}C$ signals indicative of planktonic carbon.

$\delta^{15}N$-inferred trophic positioning of benthic consumers revealed a greater relative diversity of primary consumers (detritivores, grazers) in recovered lakes, and secondary consumers (carnivores) in stressed lakes (Fig. 2.6). In stressed lakes, $\delta^{15}N$ values suggested that only Asellidae and Chironomidae functioned as primary consumers of detritus and periphyton (Fig. 2.6a). A greater diversity of acid-tolerant consumers occupied trophic positions more than one trophic level (~3.4 $\delta^{15}N$ units; Kling et al. 1992) above that of detritus and periphyton. In contrast, six families occupied trophic positions that were within one trophic level of primary carbon sources in the littoral habitats of recovered lakes (Fig. 2.6b). Specifically, asellids and hyallids functioned as primary consumers of detritus, while limnephilids, viviparids, corydalids, and cambarids fed mainly on periphyton (Fig. 2.6b).

Autotrophic community structure

Differences in total algal biomass between stressed and recovered lakes were significant (RM-ANOVA, stress, $F_{1,4} = 10.47$, $P = 0.03$) during summer 2003. Total biomass increased substantially in recovered lakes relative to that in stressed lakes following day 30 (Fig. 2.7). DIC, pH, and TDP were significant predictors of algal biomass, explaining 45.5% of the variation ($F_{3,13} = 3.62$, $P = 0.04$).

Gross taxonomic composition of autotrophs differed significantly between stressed and recovered lakes (Fig. 2.8; RM-MANOVA, time x stress, $F_{14,56} = 3.57$, $P < 0.001$). Fga made up 78 % of autotrophic biomass in stressed lakes and 87 % in recovered lakes with samples often being dominated by a single genus (e.g., *Mougeotia, Spirogyra*). Diatoms and desmids (RM-ANOVA, time x stress, desmids: $F_{2,8} = 3.54$, $P = 0.08$; diatoms: $F_{2,8} = 12.14$, $P = 0.004$) were more abundant in recovered lakes. Although not statistically significant (RM-ANOVA, stress, $F_{1,4} = 5.42$, $P = 0.08$), a higher proportion of cyanobacteria were found in stressed lakes.

CCA captured 54.4% of the total variance in species data and for 89.8% of the joint variance between algal and environmental variables and was significant ($P < 0.01$) (Fig. 2.9). Thirty-three taxa were omitted because they occurred infrequently and did not influence the final ordination. The first axis ($\lambda_1 = 0.36$) was best described by DOC ($r = -0.92$) and pH ($r = -0.69$) and explained 28.0% of the species variance. CCA axis 1 separated *Homoeothrix* (No. 3), a clear-water (i.e., low DOC) species, from desmids such as *Euastrum* (No. 10) and *Gonatozygon* (No.11) (Fig. 2.9a). In addition, the gradient contrasted acid-tolerant taxa (e.g., *Homoeothrix* [No. 3]) with acid-sensitive taxa (e.g., *Achnanthes* [No. 14] and *Gomphonema* [No.18]). Site scores distinctively separate acid lakes from recovered lakes, according to pH (Fig. 2.9b).

The second CCA axis ($\lambda_2 = 0.15$), explained 11.6% of the species variance and was positively correlated with DIC ($r = 0.40$). Site scores

suggested that DIC increased in recovered lakes during the survey period, while DIC became less available for autotrophs in stressed lakes (Fig. 2.9b). The second axis contrasted certain diatoms, *Fragilaria* (No. 17) and *Pinnularia* (No.21), with fga (*Zygogonium* [No. 29]) and desmids (e.g., *Netrium* [No. 12] and *Gonatozygon* [No. 11]). Grazer biomass was retained as an independent significant variable following forward selection, explaining 3 % of the total species variance.

Discussion

Resources or "bottom-up" factors were the primary predictors of benthic consumer and autotrophic community structure along a gradient consisting of six recovering acidified lakes. Greater nutrient availability and reduced acidity explained both increased autotrophic biomass, and taxonomic shifts in consumer and autotrophic communities. Total consumer biomass did not differ between stressed and recovered lakes because of a compensatory size-shift involving numerous, small acid-tolerant omnivores (asellids and chironomids) and fewer, large acid-sensitive omnivores (cyprinid minnows) and grazers (tadpoles). Further, consumers and autotrophic biomass were not significantly correlated and explained little variance in taxonomic composition, suggesting a weak trophic interaction (i.e., grazing) between these two communities. Below, I consider potential explanations for the observed relative importance of

abiotic and biotic regulation of consumers and autotrophic community structure in recovering acidified lakes.

Abiotic regulation of consumers

The survey showed that pH and DOC best explained patterns in consumer community structure. Specifically, cyprinids, tadpoles, gammarids, and viviparids were restricted to pH-recovered lakes with elevated DOC concentrations, while notonectids, corixids, and odonates dominated acidic, clear lakes. These findings support other studies that show distinct communities of acid-sensitive or acid-tolerant species depending on lake acidity (Schindler et al. 1985; Harvey and McArdle 1986; Carbone et al. 1998). A pH of 6 has been identified as a critical threshold for many organisms, below which water conditions can become toxic (Schindler 1988; Havens et al. 1993). Therefore, wide variation in taxa-specific physiological tolerances may explain the primacy of abiotic factors regulating consumers. Further, it is possible that aerial dispersal by many species (Keller et al. 1992; Bohonak and Jenkins 2003) has enabled them to closely track recent water quality improvements involving decreased acidity, and increased DOC and conductivity.

An increase in species size appears to be a general response of consumers to chemical recovery in our survey lakes. The community shifted towards larger-bodied consumers with the re-establishment of acid-sensitive grazers in recovered lakes, owing possibly to suitable

chemical conditions for growth and development. In contrast, increased stress tolerance or reduced energetic growth costs may explain the persistence of smaller consumers in acidified (Bilyj and Davies 1989) and other chemically polluted lakes (Cattaneo et al. 1998).

Biotic regulation of consumers

The relative minor importance of autotrophic biomass to consumers may reflect the expected prevalence of omnivory in benthic foodwebs of boreal lakes (France et al. 1998; Vinebrooke et al. 2001). The typical 3 - 4‰ enrichment in $^{15}\delta N$ per trophic level was not observed between consumers and their potential prey, which is indicative of omnivorous diets (Kling et al. 1992). In addition, several consumers had highly variable $^{13}\delta C$ values, suggesting broad feeding habits that span different trophic levels and habitats (Vander Zanden and Vadeboncoeur 2002; Herwig et al. 2004). Omnivory is hypothesized to function as an adaptive strategy as consumers may have to feed at trophic levels with available energy and biomass despite traditional feeding habits, particularly in stressed habitats (Vadas 1990). In fact, our stable isotope analyses agree with the findings by Mihuc (1997) and Dangles (2002) that show many benthic invertebrates have far more flexible omnivorous diets under stressful conditions than indicated by traditional assignment to functional-feeding groups based on mouthpart morphologies.

Use of multiple carbon sources by zoobenthos is a potential explanation for the observed lack of a relationship between consumers and benthic autotrophs. Stable isotopic analyses also showed that periphyton was not the primary carbon source for the benthic foodwebs. Specifically, $^{13}\delta C$ signatures for most consumers were more closely associated with sources of detritus (CPOM, FPOM) than with periphyton. Vinebrooke et al. (2001) also concluded that detrital-based foodwebs are likely common in the littoral zone of boreal lakes based on stable isotopic analyses. In my study, omnivorous tadpoles and cyprinid minnows were the only organisms that relied heavily on periphytic carbon based on both stable isotopic and ordination analyses. The importance of planktonic carbon sources to many consumers was also apparent in both lake groups.

Although visually feeding fish can structure littoral foodwebs (Bendell and McNicol 1995), the greater abundance of large potential prey taxa in the recovered lakes suggested sparse populations of benthivorous fish did not strongly suppress zoobenthos. In acidified lakes, acid-tolerant predatory invertebrates are expected to strongly suppress other invertebrates (e.g., Appelberg et al. 1993), thereby, possibly contributing to the observed size-shift towards smaller grazers in the stressed lakes. The highest trophic levels in the stressed lakes were occupied by notonectids, which are known to increase in abundance, along with corixids and odonates in other fishless lakes (Bendell and McNicol 1995).

Therefore, I expect that a size-shift in benthic predators from small, tolerant invertebrates to larger, sensitive fish species leads to trophic compensation, which maintains benthivory in recovering acidified lakes.

Abiotic regulation of autotrophs

Abiotic regulation of autotrophic communities in the Killarney lakes is consistent with findings from previous surveys of acid-stressed lakes (Turner et al. 1991; Vinebrooke 1996). Increased autotrophic biomass in the recovered lakes likely resulted from reduced carbon limitation owing to greater DIC availability under less acidic conditions (Turner et al. 1991). In addition, a positive relationship between DOC and autotrophic biomass suggested that DOC had a stimulatory effect on algal growth, possibly because DOC functions as a photoprotectant against DNA-damaging ultraviolet radiation (Vinebrooke and Leavitt 1996), chelator of toxic metals (Kullberg et al. 1993), and a source of carbon to heterotrophic algae (Tuchman 1996). Greater autotrophic biomass in the recovered lakes was also positively related to higher TDP concentrations, but this relationship is likely unrelated to chemical recovery because acidification does not affect TDP levels in other boreal lakes (e.g., Vinebrooke et al. 2003a).

Autotrophic communities in both stressed and recovered lakes were dominated by filamentous green algae (fga). Increased accumulations of fga in both atmospherically and experimentally acidified lakes have been well documented (e.g., Schindler et al. 1985; Turner, et

al. 1991); however, the dominance of fga has also been reported in circumneutral lakes (Gruendling 1971). Fga, such as *Mougeotia* and *Zygogonium*, are known to proliferate in the littoral zone of acid-stressed lakes because they are able to competitively obtain inorganic carbon when DIC concentrations are low under acidic conditions (Turner et al. 1987).

Distinct taxonomic shifts from cyanobacteria to desmids and diatoms occurred along gradients of increasing pH and DOC, which is typical in stressed and recovered acidified lakes (Turner et al. 1995; Vinebrooke 1996; Vinebrooke and Graham 1997). Experimental manipulation (pH 5.5 - 5.8) of Lake 302S resulted in an increased abundance of cyanobacteria (Findlay et al. 1999). Similarly, Turner et al. (1995) found that filamentous cyanobacteria accounted for almost 80% of algal composition at comparable pH levels. Circumneutral lakes often contain high abundances of diatoms, such as *Achnanthes* and *Cymbella* (Planas et al. 1989; Vinebrooke and Graham 1997). The enhanced growth of fga and desmids in recovered lakes is attributed to increased concentrations of DOC, which alleviates suppression of growth by ultraviolet radiation (Vinebrooke and Leavitt 1996). Improved chemical conditions should favor less competitive, short algal species (e.g., desmids), however, due to increased susceptibility to grazing these species often are not abundant under high grazing in recovered systems (Graham and Vinebrooke 1998).

Biotic regulation of autotrophs

The inferred effects of benthic grazers on autotrophs were subtle. Although autotrophic biomass was not a significant function of grazer biomass, I did detect a taxonomic shift from loosely-attached, grazing-sensitive fga (*Mougeotia* and *Zygogonium*) towards firmly-attached, grazer-resistant fga (*Oedogonium* and *Bulbochaete*) along the recovery gradient. Evidence from previous experiments also shows that benthic grazers often exert stronger effects on autotrophic taxonomic composition than on total biomass (Vinebrooke 1996; Graham and Vinebrooke 1998). The weak effect of benthic grazers on the total autotrophic biomass, consisting primarily of fga, is likely due to large consumers (e.g., algivorous minnows) not heavily exploiting these algae as their primary carbon source (Vinebrooke et al. 2001). Further, morphological constraints of the mouthparts of small herbivorous invertebrates could release fga from grazing pressure, enabling them to accrue large biomass in all of my study lakes.

Compensatory species dynamics and ecosystem recovery

My findings from a revisit of Killarney lakes suggested that abiotic factors remained the primary factors regulating benthic communities despite a decade of recovery having passed since similar investigations were conducted (e.g., Vinebrooke 1996; Vinebrooke and Graham 1997). The importance of abiotic factors suggested that biological recovery was

incomplete in these lakes. Alternatively, compensatory taxonomic shifts in benthic consumer communities may maintain herbivory during ecosystem recovery, thereby negating differences in grazing pressure between chemically stressed and recovered lakes. However, taxonomic shifts toward larger grazers should affect feeding selectivity, and therefore, alter autotrophic community composition. Consequently, the role of benthic grazing as an ecological mechanism regulating recovery in acid-stressed lakes still warrants further study.

Table 2.1. Water chemistry for six Killarney lakes based on samples taken from the littoral area over a 90-day survey period. Lakes are arranged in order of decreasing acidity. TN= total nitrogen; DOC= dissolved organic carbon; DIC= dissolved inorganic carbon.

Lake	Date of Survey	pH	Conductivity (um/s)	TN (µg/L)	TDP (µg/L)	DOC (mg/L)	DIC (mg/L)
Stressed							
Acid†	0	5.11	20	273.51	1.8	1.7	0.69
	30	5.36	19.8	209.97	3.5	2.17	0.77
	60	5.04	19.2	198.59	0.6	2.06	0.43
	90	5.04	19.7	244.76	1.9	2.32	0.73
Norway	0	5.2	23.3	250.73	2.3	2.16	0.45
	30	5.41	28.6	296.8	*	2.43	0.65
	60	5.46	22	206.67	0.7	1.86	0.48
	90	5.55	26.4	239.08	*	1.71	0.54
Ruth Roy†	0	6.89	49.7	273.95	4.2	3.22	3.69
	30	6.37	30.2	304.81	1.8	1.9	1.41
	60	4.85	22.3	264.22	0.9	1.55	0.35
	90	4.91	21.1	217.91	1.6	1.17	0.37
Mean		5.43	25.19	248.42	1.93	2.02	0.88
S.E.		0.18	2.46	10.23	0.35	0.15	0.27
Recovered							
AY Jackson	0	5.65	15.3	232.52	1.2	1.98	0.57
	30	6.8	23.8	304.82	*	3.16	0.91
	60	6.12	23.1	316.87	1.8	3.26	0.75
	90	6.01	23	273.51	1.4	3.5	0.67
Carlyle	0	7.14	38.9	379.24	*	3.74	2.23
	30	5.96	24.9	329.69	*	4.31	0.59
	60	6.19	27.1	278.56	2.7	4.18	0.61
	90	5.75	19	250.13	*	4.19	0.58
Little Sheguiandah	0	6.65	34.9	351.48	5.5	4.14	1.7
	30	7.35	37.2	323.08	6.5	5.16	2.64
	60	6.48	26.8	331.92	2	4.82	1.33
	90	6.91	*	314.1	2	4.65	1.83
Mean		6.42	26.73	307.16	2.89	3.92	1.2
S.E.		0.16	2.24	12.15	0.66	0.25	0.21

*data unavailable
† denotes fishless lake

Table 2.2. Significant environmental predictors of consumer and periphyton biomass based on multiple regression analysis of abiotic and biotic factors from six survey lakes.

	Consumer			Periphyton		
Effect	Coefficient	T	*P*	Coefficient	t	*P*
pH				0.88	3.14	0.008
Log conductivity						
Log TN						
Log TDP	-0.85	-3.17	0.007	-0.61	-2.16	0.05
Log DIC				-3.64	-2.23	0.04
Log DOC						
Log periphyton biomass					n/a	n/a
Log consumer biomass		n/a	n/a			
Log grazer biomass		n/a	n/a			

Table 2.3. Taxonomic composition of surveyed consumers present (+) in stressed and recovered lakes listed alphabetically by order. Large bodied consumers are denoted in capital letters within functional feeding groups. Taxon identification numbers correspond to those used in CCA plot.

Number	Order	Family	Functional Group	Stressed	Recovered
1	Amphipoda	Hyallidae	Grazer	+	+
2		Gammaridae	Grazer		+
3	Anura	Ranidae	GRAZER		+
4	Coleoptera	Dytiscidae-adult	Omnivore	+	+
5		Dytiscidae	Omnivore	+	
6		Gyrinidae	Omnivore	+	
7	Cypriniformes	Cyprinidae	OMNIVORE		+
8	Decapoda	Cambaridae	OMNIVORE	+	+
9	Diptera	Chironomidae	Omnivore	+	+
10	Ephemeroptera	Ephemerellidae	Grazer		+
†		Heptageniidae	Omnivore	+	+
†		Leptophlebidae	Grazer		+
11	Gastropoda	Viviparidae	Grazer		+
12	Hemiptera	Corixidae	Omnivore	+	
13		Notonectidae	Omnivore	+	+
†	Hydrachnida	unknown	Predator	+	+
14	Isopoda	Asellidae	Grazer*	+	+
†	Megaloptera	Corydalidae	Predator	+	+
†		Sialidae	Predator		+
15	Odonata (Anisoptera)	Libellulidae	Predator	+	+
16		Gomphidae	Predator	+	+
17	Odonata (Zygoptera)	Coenagriondae	Predator	+	+
18	Trichoptera	Limnephilidae	Grazer	+	+
19		unknown	Grazer	+	+

*primarily feeds on detritus
† excluded from CCA

Table 2.4. List of periphyton taxa used in canonical correspondence analysis (CCA). Taxon identification numbers correspond to those used in CCA plots. Periphyton is grouped into cyanobacteria (C), desmids (DE), diatoms (DI), filamentous green algae (FG), and green algae (G).

Number	Taxon	Algal group
1	*Anabaena*	C
2	*Chroococcus*	C
3	*Homoeothrix*	C
4	*Lyngbya*	C
5	*Merismopedia*	C
6	*Oscillatoria*	C
7	*Phormidium*	C
8	*Bambusina*	DE
9	*Cylindrocystis*	DE
10	*Euastrum*	DE
11	*Gonatozygon*	DE
12	*Netrium*	DE
13	*Staurastrum*	DE
14	*Achnanthes*	DI
15	*Cymbella*	DI
16	*Eunotia*	DI
17	*Fragilaria*	DI
18	*Gomphonema*	DI
19	*Navicula*	DI
20	*Nedium*	DI
21	*Pinnularia*	DI
22	*Stenopterobia*	DI
23	*Tabellaria*	DI
24	*Bulbochaete*	FG
25	*Mougeotia*	FG
26	*Oedogonium*	FG
27	*Spirogyra*	FG
28	*Stigeoclonium*	FG
29	*Zygogonium*	FG
30	*Scenedesmus*	G

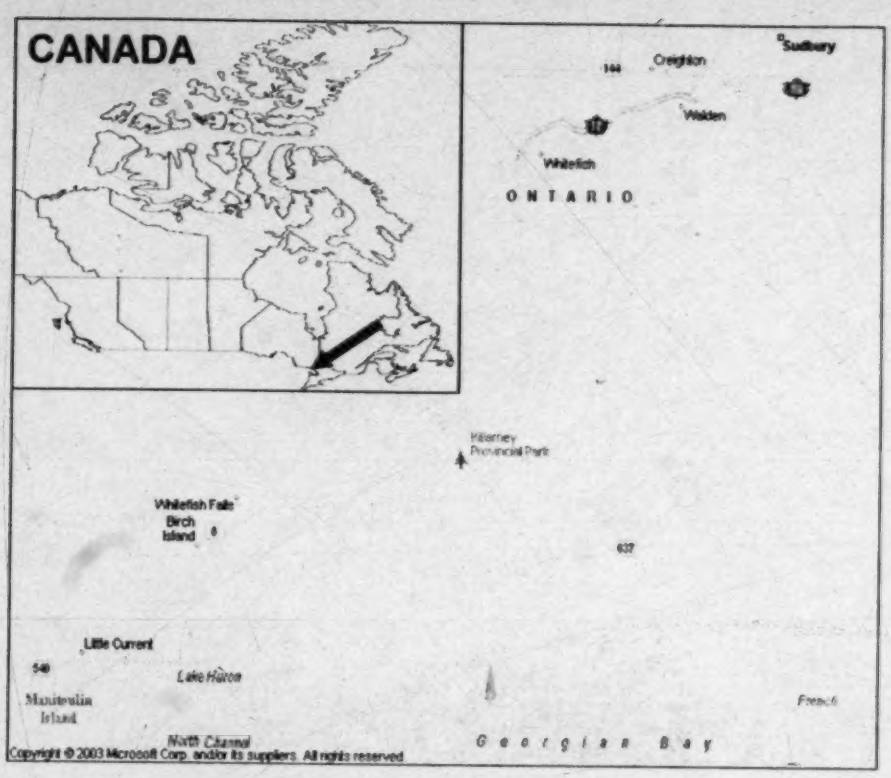


Figure 2.1. Study area showing the location of Killarney Park in Ontario, Canada.

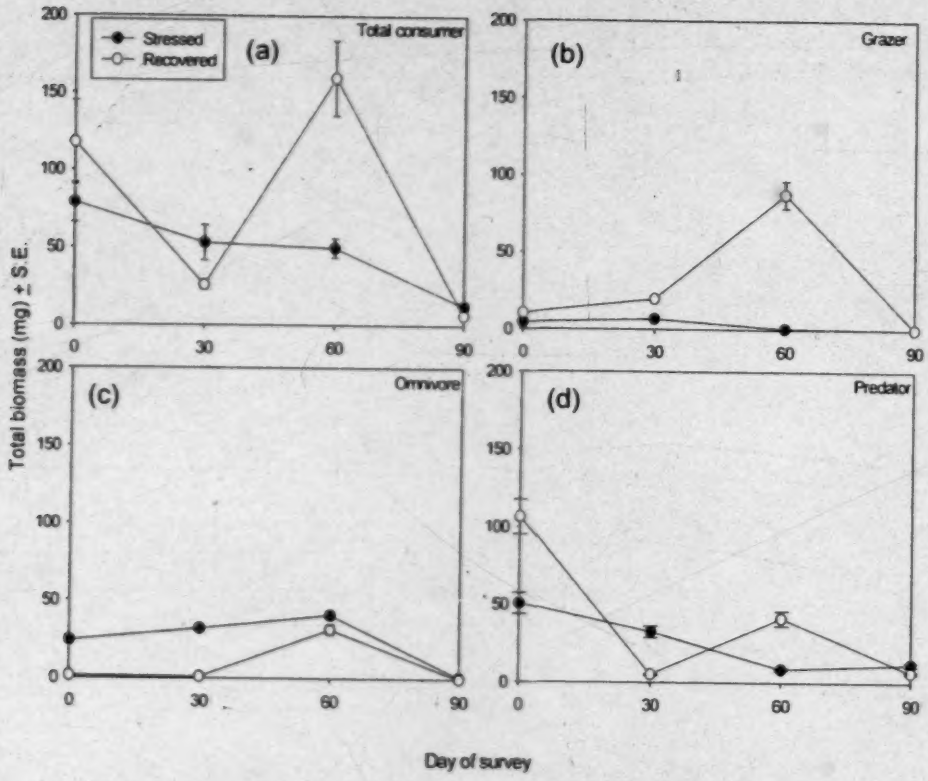


Figure 2.2. Biomass of (a) total benthic consumers divided into functional feeding groups, (b) grazers, (c) omnivores, and (d) predators in stressed (closed circles) and recovered lakes (open circles) over the 90-day survey period (n = 3).

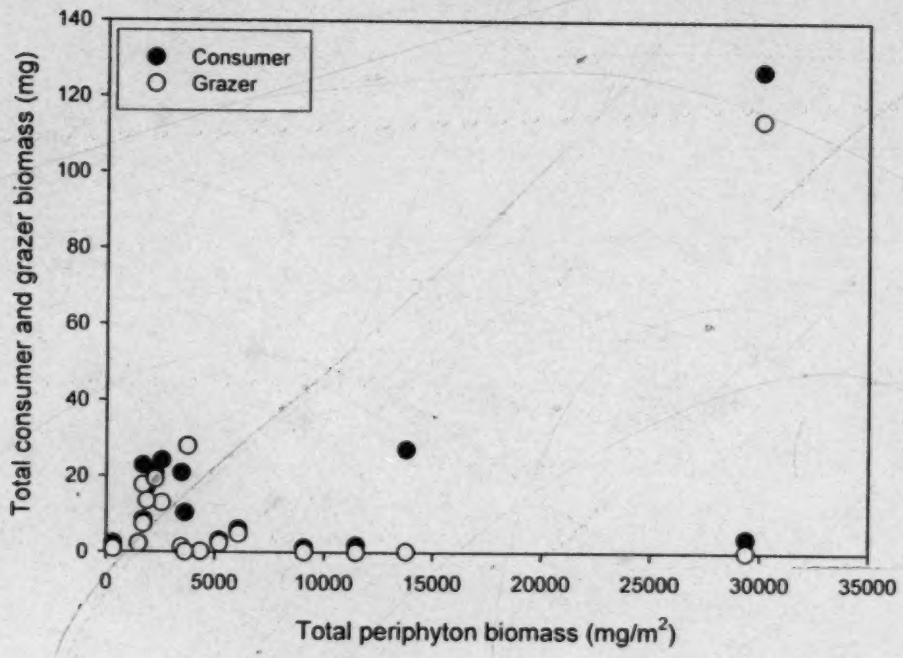


Figure 2.3. Relationship between benthic consumer and grazer biomass and periphyton biomass across survey lakes (n = 6) during summer 2003.

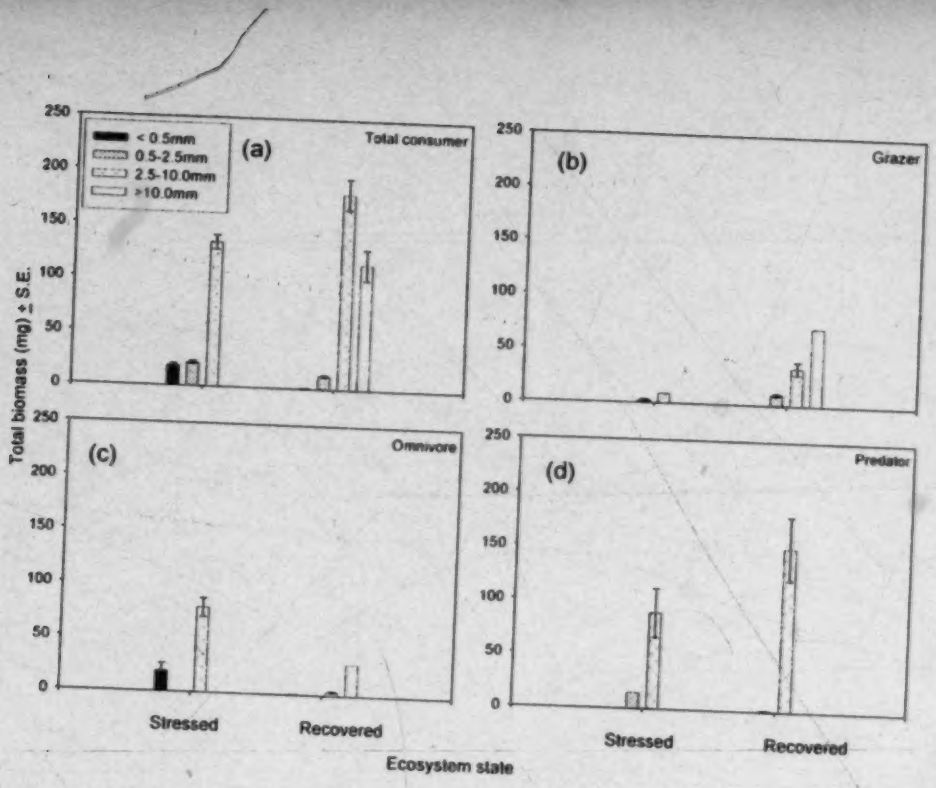
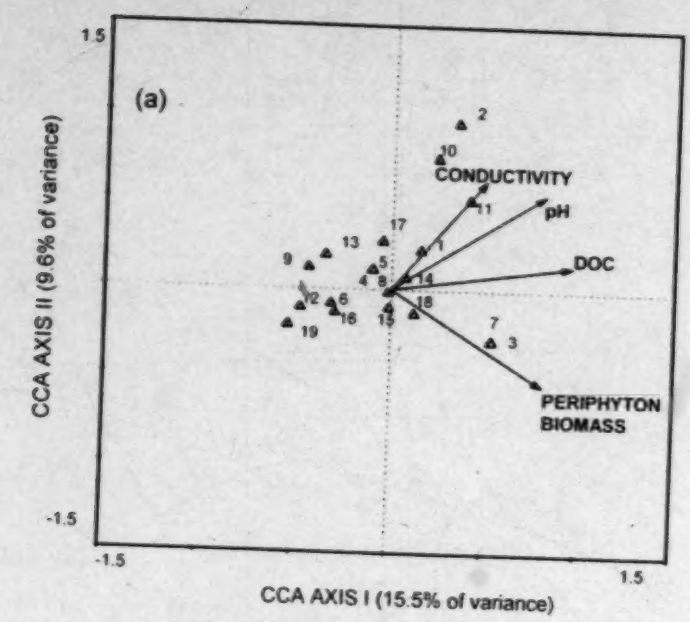


Figure 2.4. Size-structure of (a) total benthic consumer, (b) grazer, (c) omnivore, and (d) predator biomass in stressed and recovered lakes (n = 3).



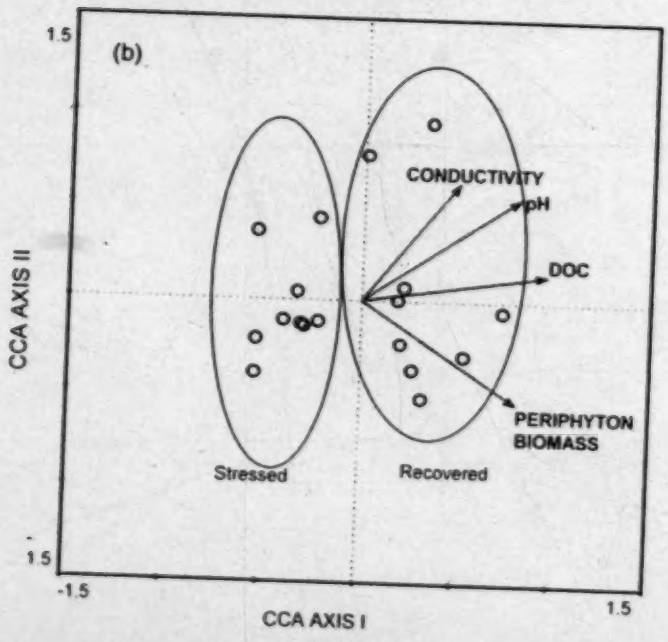


Figure 2.5. Association of (a) benthic consumer taxa and (b) sampling site scores with environmental variables based on log_{10}-transformed consumer biomass, water chemistry, and periphyton biomass data. (a) Trichopterans (No. 19) that could not be identified to family are shown separately from members of the Limnephilidae (No. 18) family.

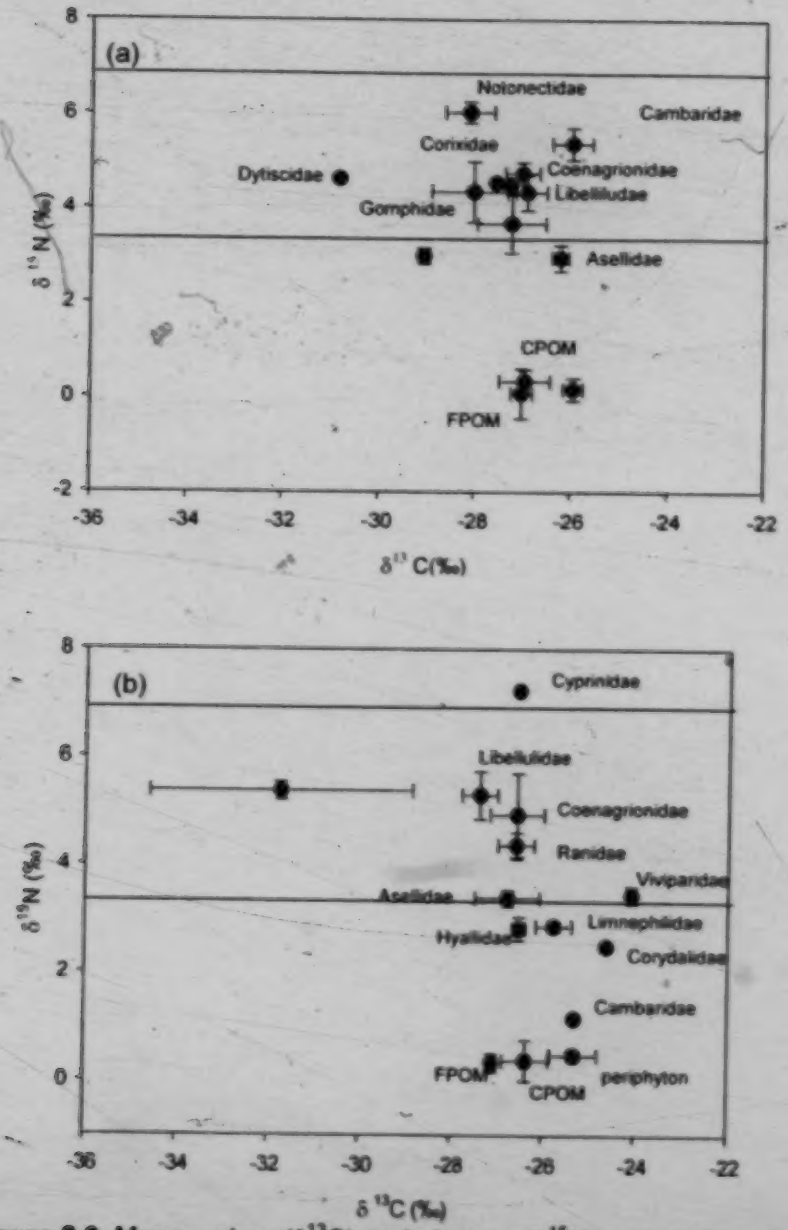


Figure 2.6. Mean carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) values (‰ ± S.E.) of periphyton, CPOM, FPOM, and benthic consumers collected from (a) stressed lakes and (b) recovered lakes (n=3) during summer 2003. Lines delineate ~3.4‰ enrichment in $\delta^{15}N$ level per trophic level.

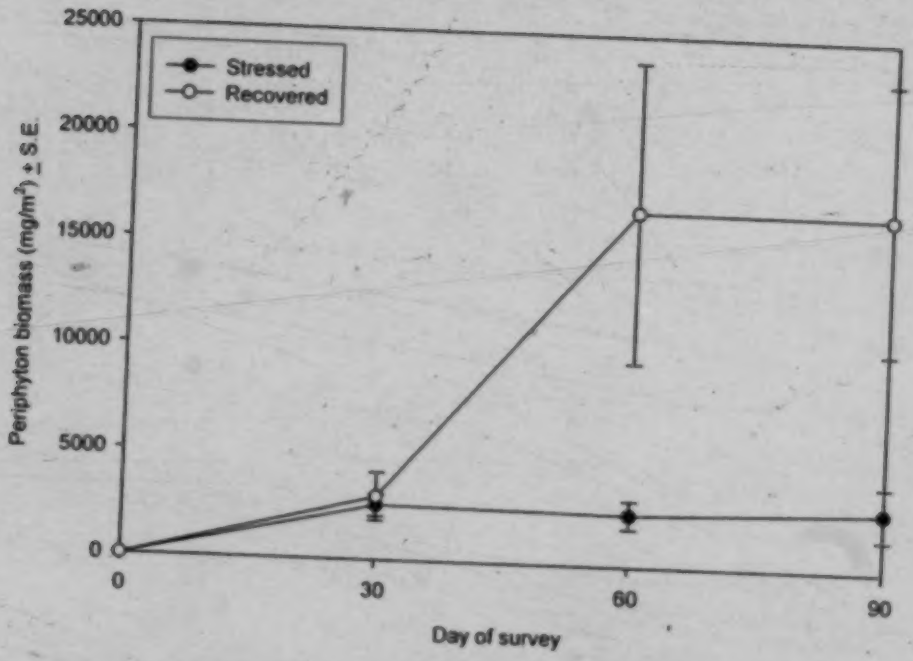


Figure 2.7. Periphyton biomass in stressed and recovered lakes over the 90-day survey period (n = 3).

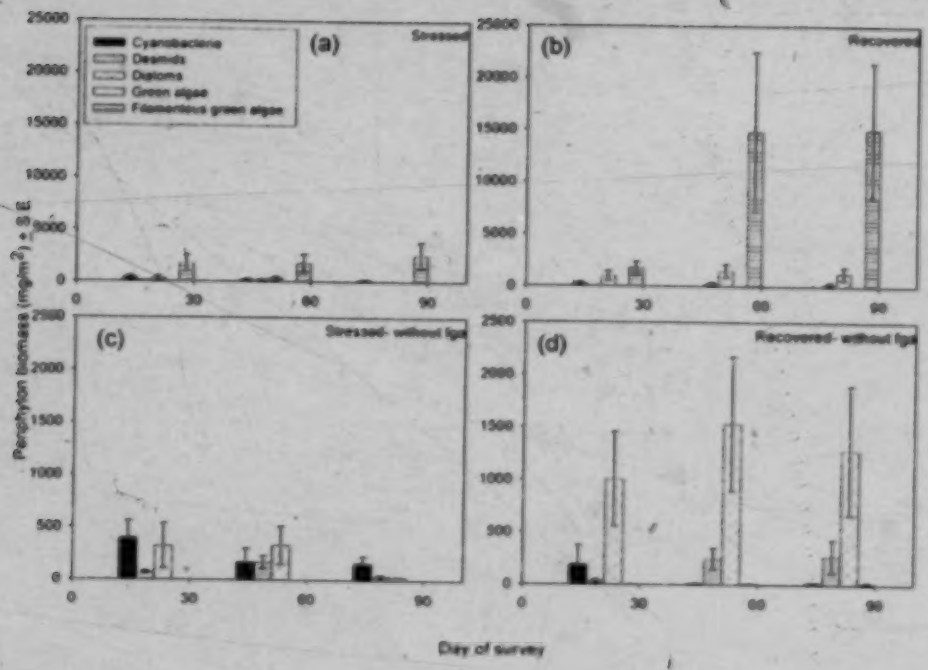


Figure 2.8. Periphyton biomass based on taxonomic group composition for stressed and recovered lakes, where (a,b) show all five taxonomic groups while (c,d) omit filamentous green algae (fga) to show trends of less dominant groups (n = 3).

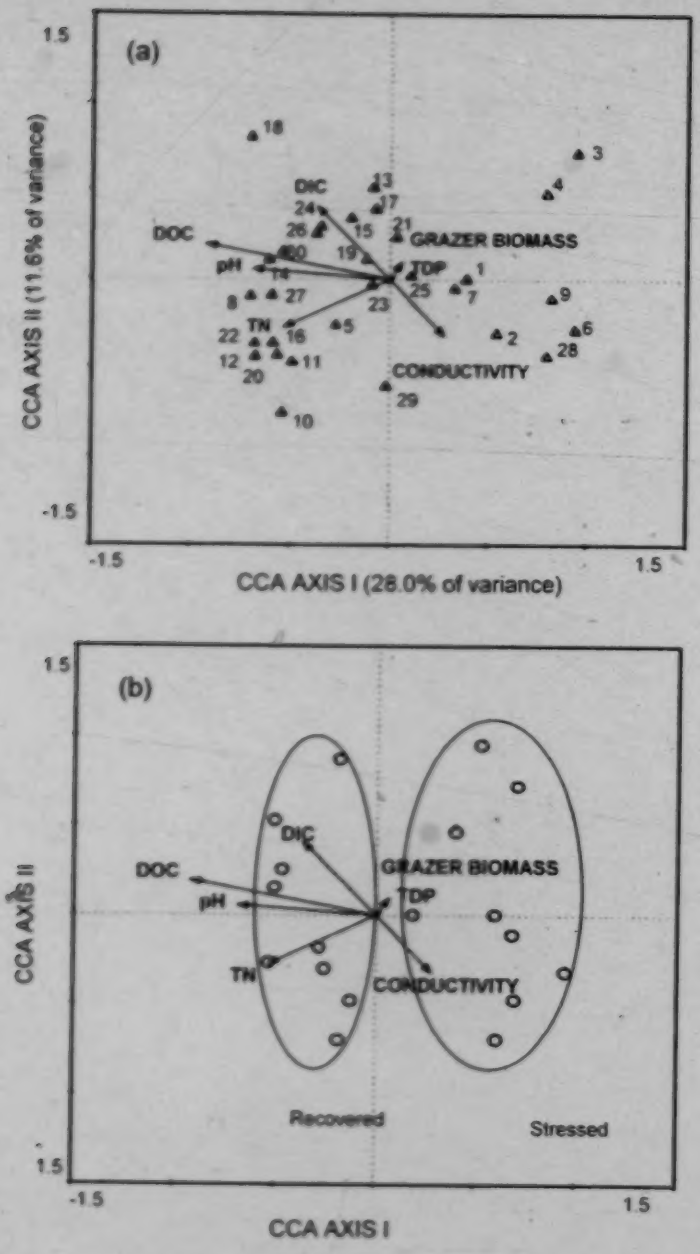


Figure 2.9. Association (a) periphyton taxa and (b) lake sampling sites with environmental variables across six survey lakes based on log_{10}-transformed periphyton taxa biovolumes, water chemistry, and grazer biomass data.

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CHAPTER THREE

BENTHIC GRAZING AND FUNCTIONAL COMPENSATION IN STRESSED AND RECOVERED LAKES

Introduction

Ecological processes performed by species-poor functional groups are expected to become more efficient as species diversity and size-structure increase during ecosystem recovery (Odum 1985). For example, diverse consumer assemblages exhibit greater exploitation of food resources (Naeem and Li 1998; Norberg 2000; Duffy 2002). Similarly, large consumers often collectively exert stronger predation pressure than do smaller stress-tolerant species (Brooks and Dodson 1965; Cattaneo and Kalff 1986; Diehl 1992; Cattaneo et al.1998). Thus, grazing has been hypothesized to increasingly structure autotrophic communities in recovering lake ecosystems owing to colonization by larger, sensitive herbivores (Fairchild and Sherman 1992; Vinebrooke et al. 2001, 2003a).

Alternatively, ecological processes may remain unchanged during ecosystem recovery owing to compensatory species replacements (i.e., functional compensation; Frost et al. 1995; Schindler 1995; Vinebrooke et al. 2003b). However, functional compensation typically does involve substantial taxonomic shifts during environmental change (Klug et al. 2000; Fischer et al. 2001; Vinebrooke et al. 2003b). Thus, benthic grazing

pressure may be maintained by fewer, but larger, sensitive species that replace numerous smaller tolerant herbivores, such as chironomids (Fig. 3.1a). Similarly, a taxonomic shift towards sensitive benthic algal taxa may compensate functionally for declines in tolerant taxa in recovering lake ecosystems (Fig. 3.1b). Further, previous studies have concluded that species diversity increases the potential for a tolerant species being present that can compensate for sensitive competitors (Walker 1992; Tilman 1996; Klug et al. 2000). Therefore, benthic functional groups containing a diverse array of species should exhibit a greater potential for functional compensation. For example, autotrophic biomass remained relatively unchanged despite the extirpation of several benthic species during the experimental acidification of a boreal lake (Turner et al. 1995; Vinebrooke et al. 2003b).

Functional compensation involving size-shifts in benthic consumer and autotrophic communities has not been addressed experimentally in anthropogenically stressed lakes. Experimental exclusion of only relatively large-bodied (> 250 µm) herbivores in stressed and recovered lakes suggested grazing pressure was more pronounced under less acidic conditions (Vinebrooke 1996; Graham and Vinebrooke 1998). Therefore, I conducted an experiment in which three size categories of benthic consumers were excluded from autotrophic communities to determine their relative impacts in stressed and recovered lakes. I hypothesized that a compensatory size shift from numerous, small tolerant consumers

towards fewer, larger sensitive consumers maintains overall grazing pressure across stressed and recovered lakes. However, I also expected that a compensatory size-shift by grazers would alter feeding selectivity, thereby affecting autotrophic community composition. Further, I predicted that relatively diverse autotrophic communities would show greater functional compensation than species-poor higher trophic groups, such as herbivores (e.g., Vinebrooke et al. 2003b).

Methods

Study area

The experiment was conducted in six lakes located in Killarney Provincial Park (46°3'N, 81°21'W), southwest of Sudbury, Ontario, Canada from May to August 2003. Reduction of anthropogenic emissions of sulphur dioxide has enabled chemical improvements to occur in many of these acid-stressed lakes (Snucins et al. 2001; Findlay 2003; Keller et al. 2003). Lakes were selected based on their acidities and potential underwater exposure to DNA-damaging ultraviolet-B radiation, which are key abiotic determinants of ecosystem recovery from anthropogenic acidification (Schindler et al. 1996; Yan et al. 1996; Keller et al. 2003). The "stressed" lake group consisted of three acidic and highly UV-transparent waterbodies (Acid, Norway, and Ruth-Roy) situated on orthoquartzite bedrock while the "recovered" group included three circumneutral, relatively UV-protected lakes (A.Y. Jackson, Carlyle, and

Little Sheguiandah) located in lowland areas with limestone, granite, or sandstone bedrock (Snucins et al. 2001).

Lake water chemistry

Chemical analyses were performed on water samples collected monthly during summer 2003 from the littoral study area within each lake. Duplicate samples were analyzed at the Limnology Laboratory at the University of Alberta (Alberta, Canada). In the lab, pH was measured using a Fischer Accumet model 925 meter and compared to values recorded during summer sampling. Conductivity was determined using on a Radiometer/Copenhagen model CDM83 meter. Samples for total nitrogen (TN) samples were predigested with alkaline potassium persulfate according to Ameel et al. (1993) and determined by flow injection analysis on a Technicon™ Autoanalyzer™. Total dissolved phosphorus (TDP) was measured using standard colorimetric procedures following digestion with potassium persulfate (Menzel and Corwin 1965). DOC and DIC were both analyzed using a Shimadzu TOC-5000A analyzer.

Consumer community collection and classification

Zoobenthos were collected monthly from the shallow (~1-m depth) littoral zone using a D-frame kicksweep net (500-µm mesh size). Three time-standardized D-net sweeps were performed along a 10-m transect

adjacent to the experimental site in each lake. Samples were pooled and stored in coolers until sorting was performed later in the day. Predatory benthic consumers were immediately separated from the samples during sorting. A dissecting microscope was used at 40x and 100x magnifications to sort taxonomically all invertebrates to the family level. Many consumer specimens were collected as early instars and were difficult to identify to genus or species, therefore family level was used for all statistical analyses. Consumer body size was measured at the widest part of the body (usually head or abdomen) and was divided into four size classes (< 0.5mm, 0.5 - 2.5mm, 2.5 -10 mm, and >10 mm) based on accessibility into the different experimental exclosures (see below). After drying at 60°C for 96 h, samples were weighed. Dry weight for snails and crayfish were shell-free.

Experimental Design and Set-up

A two-factor split-plot design with repeated measures (Fig. 3.2) was used to determine the effects of chemical recovery and size structure of benthic consumer communities on autotrophic biomass and species composition. The stress treatment (plot) consisted of two levels (stressed pH~5, recovered pH~7) that were replicated three times for a total of six lakes. The lakes served as independent experimental units because they were not physically connected by waterways. Four consumer treatment levels (subplot) were created using open, coarse (10 mm), intermediate

(2.5 mm), and fine (0.5 mm) mesh exclosures. Partial cages for each treatment level were also deployed to account for the physical presence of the exclosure material (i.e., cage effect). Each exclosure contained a matrix of twelve unglazed ceramic tiles (56.25 cm^2 each), which simulated the predominant type of algal habitat (quartzite/granite bedrock) that exists along the shallow shorelines of the study lakes. All ceramic tiles were acid washed (10% HCl) for 48 h prior to deployment. Experimental exclosures were deployed in early May 2003. Each exclosure unit was randomly distributed along a south-facing, submerged rock ledge at a 0.5-m depth and secured using bricks.

Sampling and enumeration of autotrophs

Four tiles from each exclosure were retrieved randomly and processed monthly. Autotrophic communities (periphyton) were removed from the tiles with a hard-bristled toothbrush, rinsed with filtered lake water and pooled together. The harvested material was transferred from the tray to a 500-mL graduated cylinder and was filled to 200 mL with filtered lake water. The top of the cylinder was covered and inverted several times to mix thoroughly and was subsampled in the following sequence: 50 mL was filtered and concentrated on Whatman GF/C glass microfiber filter papers and frozen for chlorophyll *a* analysis and 100 mL was preserved with Lugol's solution for taxonomic analysis.

Algal biomass was quantified using fluorimetry and biovolume estimates (Wetzel and Likens 2000). For chlorophyll *a* (Chl *a*) determinations, periphyton samples were extracted in 95% ethanol for 24 h. Tubes were centrifuged at 5°C, 4400 RPM for 10 minutes and dilutions, if required, were made with 95% ethanol. Extracts were read on a Shimadzu Model RF-1501 spectrofluorophotometer at 436 nm and 680 nm, using a 1cm path-length quartz cell. For biovolume estimates, samples were well mixed and diluted depending on the density of algal and detrital material. After 1 h of settling into the base of an Utermöhl chamber, a minimum of 300 viable cells were counted under 400x or 1000x magnification on an inverted microscope. Cell viability was based on chloroplast integrity for eukaryotic cells and pigmentation for cyanobacteria. Cell counts were converted to biovolumes by approximating cell volume using geometric formulae (Hillebrand et al. 1999; Sun and Liu 2003). Biovolume was estimated on a per-cell basis for solitary and filamentous cells. A minimum of 20 cells per taxon was used to determine the mean dimensions used in geometric formulas, where sufficient cell numbers were available. Algal biovolume estimates were converted to biomass assuming the specific gravity equaled one. Mean biovolume of duplicate or triplicate enumerations are reported.

To assess autotrophic community structure, taxa were grouped into four physiognomic groups, namely firmly-attached tall, firmly-attached short, loosely-attached tall, and loosely-attached short (Table 3.1). Firmly-

attached taxa with stalked attachment or an obvious attachment structure (e.g., basal holdfast cells) were separated from those with weakly adhering capabilities. Erect and filamentous taxa were classified as tall compared to adnate or prostrate taxa, which closely adhered to the substrate or those which were found in short stalks. Physiognomy is an important determinant of how benthic autotrophs respond to abiotic and biotic factors, such as resource availability, competitive ability, and sensitivity to grazing (Steinman 1996; Graham and Vinebrooke 1998).

Algal samples were identified to genus according to Prescott (1982) and Wehr and Sheath (2003). Duplicate counts of each sample were done and if species richness (i.e., number of species) varied by more than 20%, a triplicate sample was counted.

Statistical analyses

All data were $\log_{10}$-transformed to meet assumptions of normality and homogeneity of variances. Repeated measures analysis of variance (RM-ANOVA) was used to evaluate the effects of chemical stress and size selective grazing on algal biomass using Chl *a* and biovolumes response variables and to test for the effect of partial cages (Scheiner and Gurevitch 2001). Lake pH status was included as a between-plot factor and grazer treatment level was included as a within-plot factor. Statistical analysis was performed with SYSTAT Version 10 (SPSS 2000) using the general linear model (GLM) procedure. If the assumption of sphericity was

violated, we used conservative Greenhouse-Giesser corrected significance levels. Repeated-measures multivariate analysis of variance (RM-MANOVA) was used to determine differences in the functional composition of the autotrophic communities between stressed and recovered lakes and grazer treatment levels.

Canonical correspondence analysis (CCA) was conducted using CANOCO version 4.51 (ter Braak and Smilauer 2003) to examine the effect of water chemistry variables and grazer biomass on algal community composition. All algal, grazer, and water chemistry data, with the exception of pH, used in the ordination were $\log_{10}$-transformed to stabilize variances (Morin and Cattaneo 1992) and to reduce the influence of large-celled taxa (e.g., filamentous green algae), which would have dominated the ordination (ter Braak 1986). To remove ecologically irrelevant and insignificant or redundant environmental variables, data was screened prior to the final CCA using forward selection. Monte Carlo permutation testing (499 iterations) was used to test for the statistical significance of the final ordination. Algal taxa that did not occur in at least three samples were excluded from ordination analysis.

Results

Water chemistry

The stress treatment involved substantial differences in water chemistry between the two lake groups (Table 3.2). Stressed and

recovered lakes differed by approximately a full pH unit. Recovered lakes also contained higher concentrations of both autotrophic resources, such as DIC and TDP, and photo-protective DOC. Conductivity and TN levels were similar across all six lakes.

Consumer communities

Most consumers in the stressed and recovered lakes could only access the coarse-meshed and open exclosures (Fig. 3.3). In both lake groups, only chironomids and hydrachnids could enter fine-meshed exclosures. In recovered lakes, a greater diversity of consumers could enter intermediate- (e.g., ephemerellids, heptagenids, gammarids) and coarse-meshed (e.g., amphipods, viviparids) exclosures.

The exclosure treatment reduced (RM-ANOVA, exclosure, $F_{3,4}$= 10.41, P = 0.02) potential exposure of autotrophic communities to all consumers, and grazers ($F_{3,4}$= 5.74, P = 0.06) during the entire experiment (Fig 3.4). Multiple pairwise comparisons (Tukey's HSD) revealed significant differences in grazer biomass between each treatment level (P = 0.005), with biomass increasing as exclosure size increases. However, potential exposure to consumers did not differ significantly between acidified or recovered lakes for all total consumers (RM-ANOVA, time x exclosure x stress, $F_{6,40}$ = 1.6, P = 0.19) or grazers ($F_{6,40}$ = 0.7, P = 0.67). There was an apparent shift from smaller grazers (chironomids) in stressed lakes to fewer, but larger taxa (mayflies, tadpoles, minnows) in

recovered lakes (Fig. 3.4c, d), however it was not statistically significant ($P > 0.05$).

Consumer and stressor effects on autotrophic biomass

Exclusion of different size categories of consumers did not affect significantly autotrophic biomass in either stressed or recovered lakes (RM-ANOVA, time x exclosure x stress: $F_{18, 20} = 0.7$, $P = 0.81$; Fig. 3.5). In particular, total algal biomass did not differ significantly ($t = 0.76$, $df = 7$, $P = 0.47$) between fine-meshed exclosures and open controls by day 90 of the experiment. There was no difference in Chl-inferred biomass between the partial-cage treatments and open controls (RM-ANOVA, $F_{6,28} = 0.5$, $P = 0.80$).

Chemical stressors significantly suppressed autotrophic biomass based on differences in chlorophyll (RM-ANOVA, stress, $F_{1,3} = 28.4$, $P = 0.01$) and algal biovolume ($F_{1,3} = 31.2$, $P = 0.01$) between communities in stressed and recovered lakes (Fig. 3.6). At the end of the experiment, both metrics revealed positive algal growth had occurred in the recovered lakes, while remaining relatively unchanged in the stressed lakes (Fig. 3.6). Chl-*a* and algal biovolume were positively correlated across all treatments ($R^2 = 0.25$, $P < 0.001$).

Consumer and stressor effects on autotrophic community composition

The physiognomic structure of autotrophic communities did not differ significantly between stressed and recovered lakes, or the four exclosure types (RM-MANOVA, time x stress x exclosure, $F_{33,176} = 0.7$, $P = 0.85$). Loosely-attached tall and short taxa were the dominant algal forms across all treatments (Fig. 3.7).

A total of 62 algal genera from six major taxonomic groups (cyanobacteria, greens, chrysophytes, filamentous green algae [fga], diatoms, and desmids) were detected in the experiment. Chrysophytes made up less than 1% of total algal biomass and were excluded from further analysis. Chemical stress significantly altered algal composition based on changes in the relative abundance of algal groups (Fig. 3.8; RM-MANOVA, time x stress, $F_{14,308} = 8.25$, $P < 0.001$). Specifically, significantly more desmids (RM-ANOVA, stress, $F_{1,22} = 21.21$, $P < 0.001$), diatoms ($F_{1,22} = 53.95$, $P < 0.001$), fga ($F_{1,22} = 13.61$, $P = 0.001$), and greens ($F_{1,22} = 9.50$, $P = 0.05$) but not cyanobacteria ($F_{1,22} = 1.02$, $P = 0.32$) occurred in recovered lakes. Exclosures did not alter gross algal composition (RM-MANOVA, time x exclosure, $F_{42,280} = 0.32$, $P = 0.97$).

Chemical stressors significantly altered algal taxonomic composition at the genus-level based on CCA (Fig. 3.9). CCA was performed on 49 genera that accounted for 99% of the total algal biovolume across all experimental exclosures (Table 3.1). Fourteen

genera were excluded from analysis as they occurred in less than three samples. The first CCA axis explained 18.7% of the total variance in average total autotrophic biomass (Fig. 3.9a). CCA axis 1 ($\lambda_1 = 0.30$) represented a significant gradient ($F = 13.79$, $P < 0.005$) that was best described by DOC ($r = -0.95$) and pH ($r = -0.79$). The first axis contrasted genera (*Nodium* [No. 32], *Pleurotaenium* [No. 20], and *Pinnularia* [No. 33]) that were common in recovered lakes from filamentous green algae (*Zygogonium* [No. 45] and *Stigeoclonium* [No. 44]) and desmids (*Actinotaenium* [No. 10] and *Cylindrocystis* [No. 14]) that were more abundant in the stressed lakes.

Grazers also significantly influenced autotrophs at the genus-level (Fig. 3.9a). Grazer biomass was retained as an independent, significant explanatory variable that was correlated ($r = 0.41$) with CCA axis 2 ($\lambda_2 = 0.10$). The second CCA axis explained 9% of the total taxonomic variance, and was also related to DIC ($r = 0.78$) and conductivity ($r = 0.56$). CCA axis 2 separated grazer-resistant firmly-attached genera (*Gomphonema* [No. 29], *Achnanthes* [No. 23], and *Bulbochaete* [No. 39]) in recovered lakes from more edible loosely-attached taxa, such as *Lyngbya* (No.4) and *Penium* (No. 19) in stressed lakes.

Discussion

My results provided partial support for the hypothesis that herbivore-size shifts enable functional compensation that maintains

benthic grazing pressure across stressed and recovered lakes. Numerous smaller grazers (chironomids) in stressed lakes were replaced by fewer, large taxa (ephemeropterans, tadpoles, minnows) in recovered lakes, which negated a significant difference in total grazer biomass between the two lake types. However, I did not detect significant grazing effects by excluding consumers from autotrophic communities in stressed or recovered lakes. Instead, grazing effects were only detected at the taxonomic level in recovered lakes. In contrast, abiotic stressors significantly suppressed autotrophic biomass and altered taxonomic composition in the stressed lakes. Therefore, my findings suggest that benthic autotrophs are capable of functional compensation in response to weak disturbance (e.g., low grazing pressure), but not chronic stress associated with anthropogenic acidification. Below, I consider potential explanations for weak benthic grazing effects and differences in functional compensation by autotrophs to abiotic stress and grazing in relatively unproductive lakes.

Benthic grazing may have been difficult to detect in these lakes because consumer-algal interactions are inherently weak in oligotrophic systems (Elser and Goldman 1991; Lamberti 1996). Low productivity combined with predation by benthivores (e.g., crayfish, odonates) can suppress smaller herbivorous invertebrate populations, thereby minimizing their effect on autotrophs in stressed fishless lakes (Appelberg et al. 1993). Further, the prevalence of omnivory (Gu et al. 1997) and flexibility

in feeding strategy (Dangles 2002) likely weaken the reliance of many grazers on autotrophic communities in stressed ecosystems. For example, stable isotopic analyses reveal that most benthic invertebrates are not obligate herbivores in unproductive lakes (Vander Zanden and Rasmussen 1999; Vinebrooke et al. 2001; Chapter 2). Therefore, low population densities of omnivorous benthic invertebrates likely often preclude detection of grazing effects in oligotrophic systems.

High abundances of grazer-sensitive autotrophs in all lakes also indicated weak ambient grazing pressure during the study. Specifically, tall filamentous algae were abundant in both stressed and recovered lakes despite their reported susceptibility to large-bodied grazers (Gelwick and Matthews 1992; Vinebrooke 1996; Graham and Vinebrooke 1998). Compensatory shifts involving edible (zygnematacean taxa) and relatively grazer-resistant filamentous algae (oedogoniacean taxa) may also have offset the effects of benthic grazers on algal biomass (e.g., Vinebrooke 1996; Graham and Vinebrooke 1998).

Alternatively, lack of statistically significant grazing effects of autotrophic biomass may have been a consequence of low study power. Thus, I performed a post hoc power analysis using a conventional effect size of 0.8 (Quinn and Keough 2002). Based on my level of replication (n = 3), power analysis revealed an approximate 55% probability of detecting an 80% difference in autotrophic biomass between our open controls and fine-meshed exclosures. Further, my level of replication would have had

to been at least doubled (i.e., n = 6 or 12 lakes) to detect a significant grazer effect on autotrophic biomass given the variance between replicates. Morin and Cattaneo (1992) recommended a minimum level of replication of 20 for benthic algal studies using biomass as their response variable, indicating that intense sampling would be required to detect weak grazing effects.

Nevertheless, my analyses showed that relatively large grazers in recovered lakes significantly affected autotrophic community composition. This finding agreed with correlations between body-size and feeding-selectivity of benthic grazers (France et al. 1991; Vinebrooke 1996; Graham and Vinebrooke 1998). Also, Cattaneo and Kalff (1986) showed that large invertebrate grazers altered benthic algal assemblages by selectively feeding on large diatoms and filamentous algae, while not affecting total biomass. In contrast, studies in recovering acidified lakes have shown that high abundance of large benthic grazers can suppress algal biomass (Graham and Vinebrooke 1998). Similarly, Heneberry (1997) reported that the lack of large grazers (e.g., crayfish) resulted in massive accumulation of autotrophic biomass in acid-stressed lakes.

Contrary to the expectation that more diverse autotrophic communities would exhibit greater functional compensation than consumers (Klug et al. 2000; Vinebrooke et al. 2003b), abiotic stress significantly suppressed only autotrophic biomass. The spatial and temporal extent of widespread acidification over several decades may

have limited the compensation potential of benthic autotrophs by depleting the regional species pool (Minns et al. 1990; Arnott et al. 2001; Vinebrooke et al. 2003b). In contrast, Findlay et al. (1999) and Vinebrooke et al. (2003b) have documented recovery by benthic autotrophs from an 8-yr experiment in which acid was added to a single lake located among other pristine lakes. Further, small acid-tolerant autotrophs may not fully compensate for larger sensitive taxa, in terms of total biomass (Cattaneo et al. 1998; Klug et al. 2000).

The difference between the impacts of benthic consumers and abiotic stress on autotrophic biomass versus community composition highlight the strong capacity of algae to compensate for weak, natural disturbances (e.g., grazing) but not chronic, novel disturbances (e.g., anthropogenic acidification). Therefore, we must consider interactions among abiotic stressors and altered trophic interactions to predict community responses to long-term stress (Frost et al. 1995; Hulot et al. 2000).

Table 3.1. List of periphyton taxa used in canonical correspondence analysis (CCA). Taxon identification numbers correspond to those used in CCA plots. Periphyton is grouped into cyanobacteria (C), chrysophytes (CHR), desmids (DE), diatoms (DI), filamentous green algae (FG), and green algae (G). Periphyton is also grouped as loose/short (LS), loose/tall (LT), firm/short (FS), and firm/tall (FT) based on physiognomy.

Number	Taxon	Algal group	Physiognomic group
1	*Anabaena*	C	LS
2	*Aphanocapsa*	C	LS
3	*Chroococcus*	C	LS
4	*Lyngbya*	C	LS
5	*Merismopedia*	C	LS
6	*Oscillatoria*	C	LS
7	*Phormidium*	C	LT
8	*Rhaboderma*	C	LS
9	*Dinobryon*	CHR	LS
10	*Actinotaenium*	DE	LS
11	*Bambusina*	DE	LT
12	*Closterium*	DE	LS
13	*Cosmarium*	DE	LS
14	*Cylindrocystis*	DE	LS
15	*Desmidium*	DE	LT
16	*Euastrum*	DE	LS
17	*Gonatozygon*	DE	LS
18	*Netrium*	DE	LS
19	*Penium*	DE	LS
20	*Pleurotaenium*	DE	LS
21	*Staurastrum*	DE	LS
22	*Xanthidium*	DE	LS
23	*Achnanthes*	DI	FS
24	*Actinella*	DI	FS
25	*Cymbella*	DI	FS

Table 3.1. (continued)

Number	Taxon	Algal group	Physiognomic group
26	*Eunotia*	DI	LS
27	*Fragilaria*	DI	LT
28	*Frustulia*	DI	LS
29	*Gomphonema*	DI	FT
30	*Melosira*	DI	LT
31	*Navicula*	DI	LS
32	*Nedium*	DI	LS
33	*Pinnularia*	DI	LS
34	*Semiorbis*	DI	LS
35	*Stenopterobia*	DI	LS
36	*Surirella*	DI	LS
37	*Synedra*	DI	FS
38	*Tabellaria*	DI	LS
39	*Bulbochaete*	FG	FT
40	*Klebsormidium*	FG	LT
41	*Mougeotia*	FG	LT
42	*Oedogonium*	FG	FT
43	*Spirogyra*	FG	LT
44	*Stigeoclonium*	FG	FT
45	*Zygogonium*	FG	LT
46	*Chlamydomonas*	G	LS
47	*Pediastrum*	G	LS
48	*Scenedesmus*	G	LS
49	*Stichococcus*	G	LS

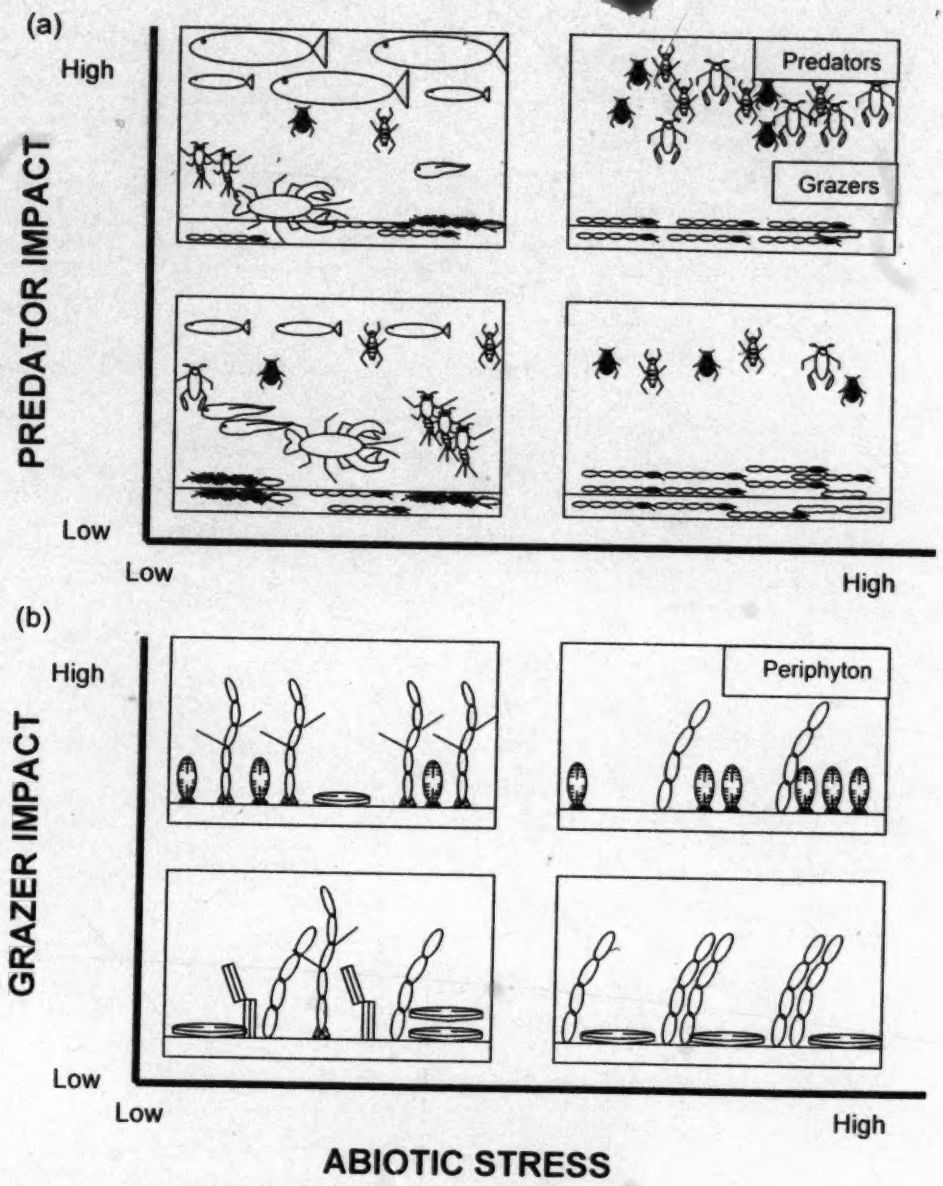

Fig. 3.1. Conceptual model showing compensatory responses by (a) consumer species to abiotic stress and predation and by (b) periphyton species to abiotic stress and grazing. Compensatory shifts (taxonomic or size) often maintain trophic processes, such as predation (a) or primary production (b) but cause substantial changes in community composition.

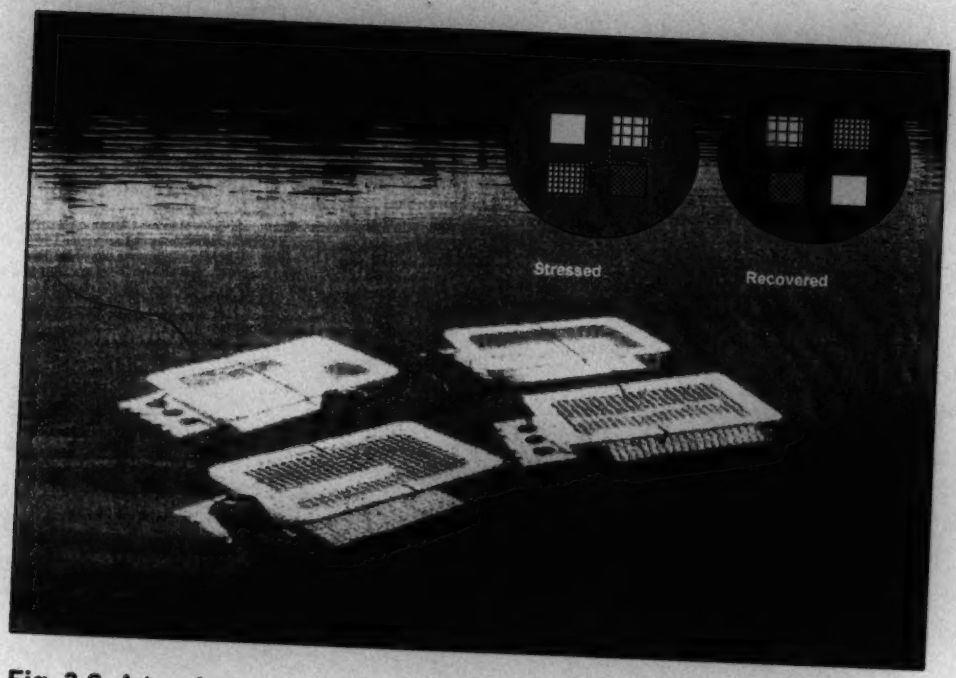

Fig. 3.2. A two factor (2 stress levels x 4 exclosure levels) experiment with split-plot (lake) design and repeated measures was performed across 3 stressed and 3 recovered lakes. Four exclosures with different size mesh (0.5mm, 2.5mm, 10.0mm, and open) and three partial cages were deployed in each lake. Each exclosure, containing 12 ceramic tiles, was weighted with bricks to reduce possible disturbance by animals and humans.

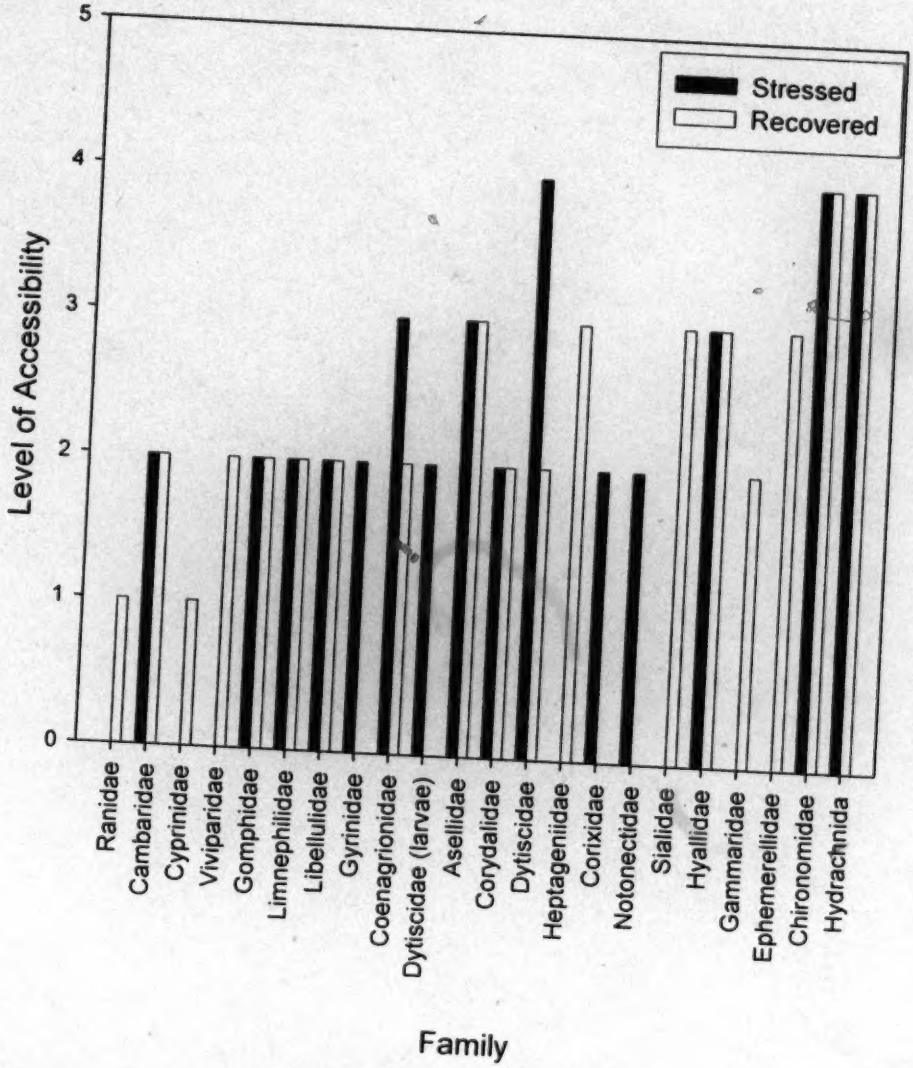

Fig. 3.3. Level of accessibility to experimental exclosures for consumer families, where 4 = fine, 3 = intermediate, 2 = coarse, 1 = open.

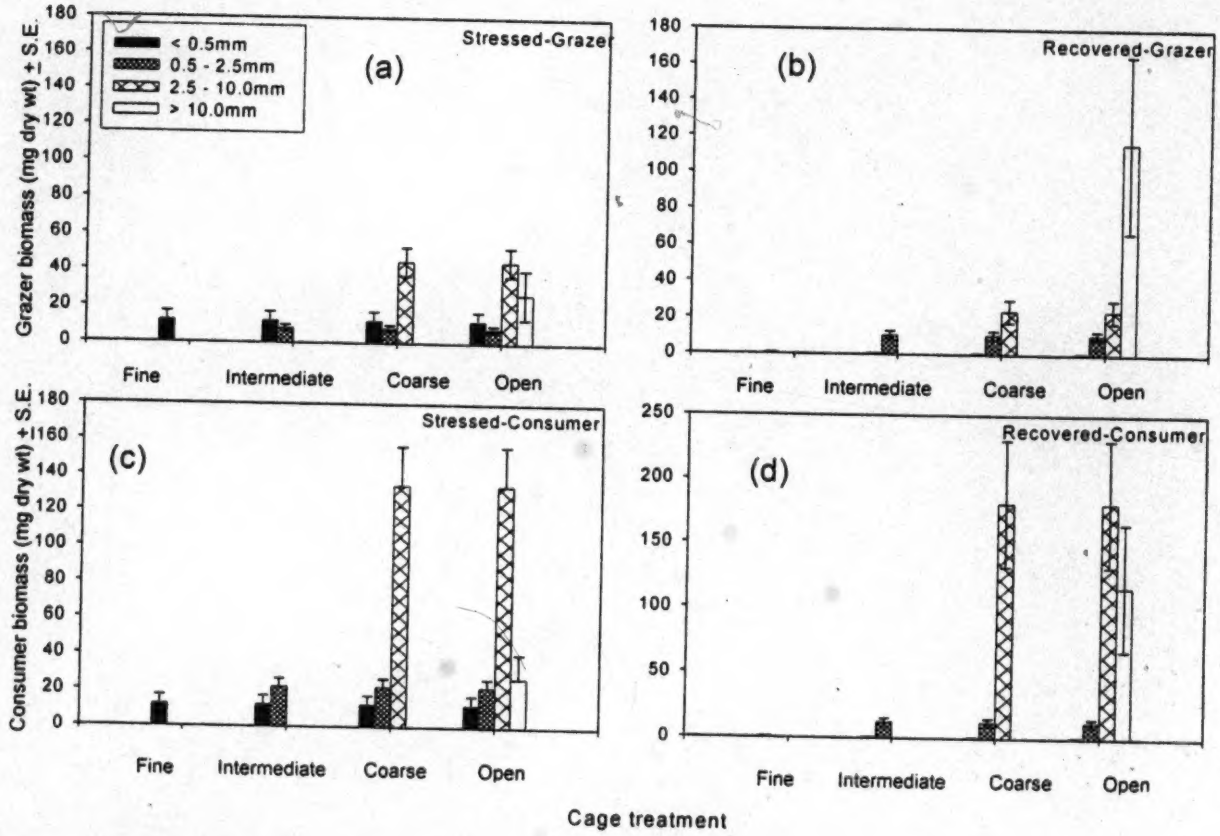

Fig. 3.4. Biomass of each size fraction of the (a,b) grazer and (c,d) consumer community that can access each exclosure treatment level.

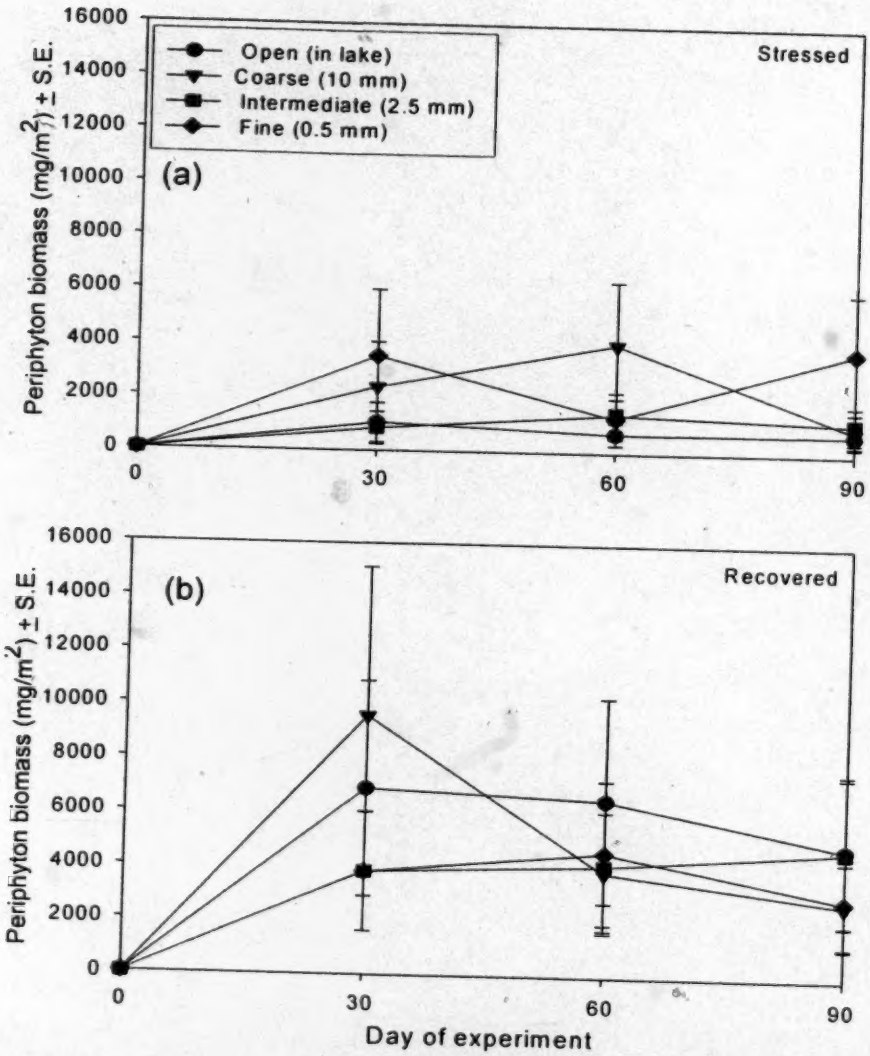

Fig. 3.5. Periphyton biomass in each exclosure in (a) stressed lakes (n=3) and (b) recovered lakes (n=3) over the 90-d experiment.

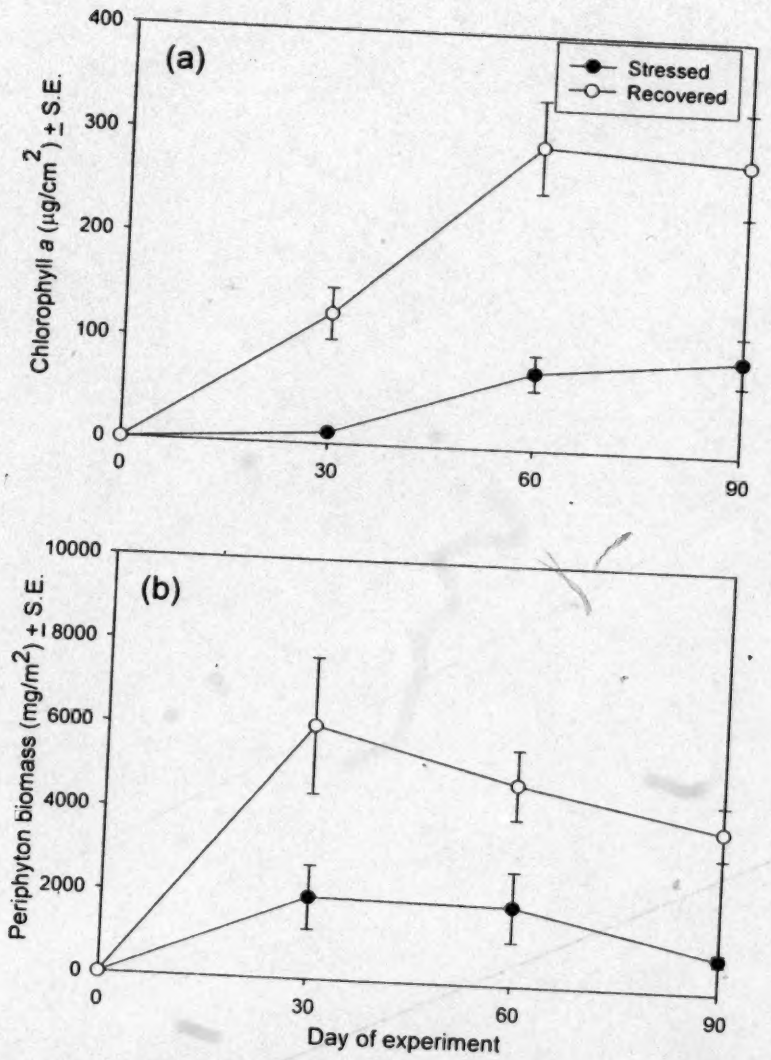

Fig. 3.6. Chlorophyll *a* (a) and periphyton biomass (b) in stressed and recovered lakes over the 90-day experiment.

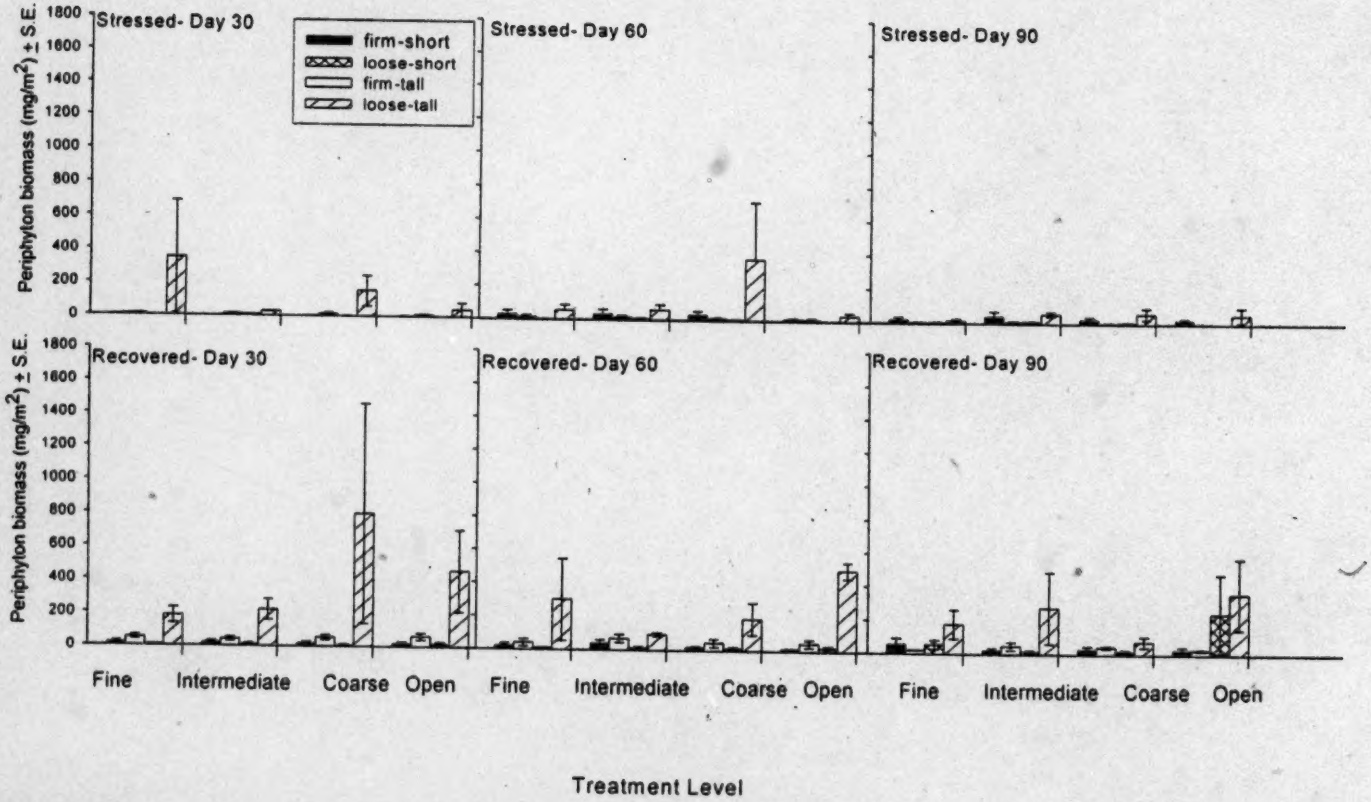

Fig. 3.7. Periphyton biomass based on physiognomic groups in stressed lakes (a-c) and in recovered lakes (d-f) for each exclosure treatment level.

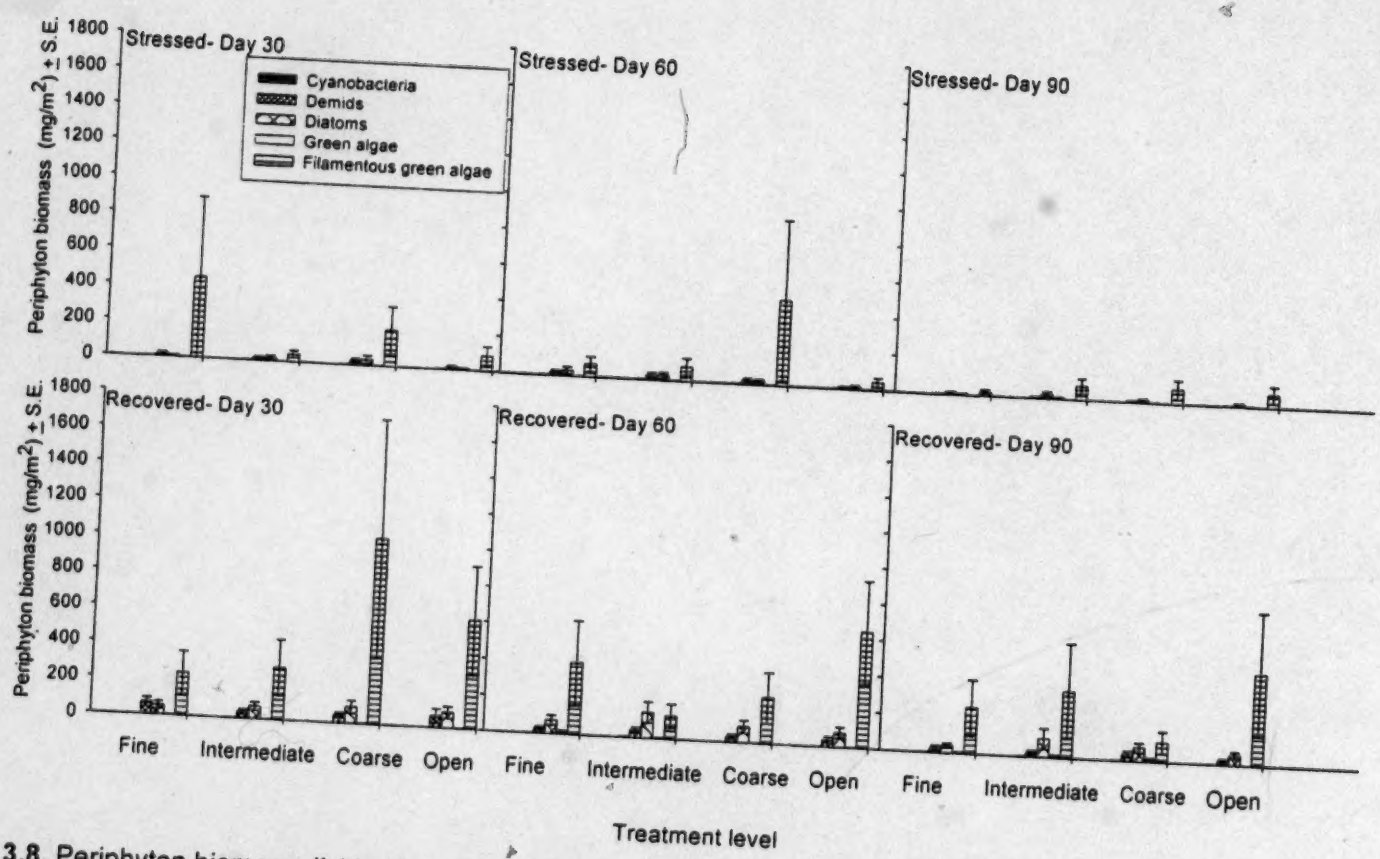

Fig. 3.8. Periphyton biomass divided into taxonomic groups found in different exclosure treatments in stressed (a-c) and recovered lakes (d-f) over the 90-day experiment.

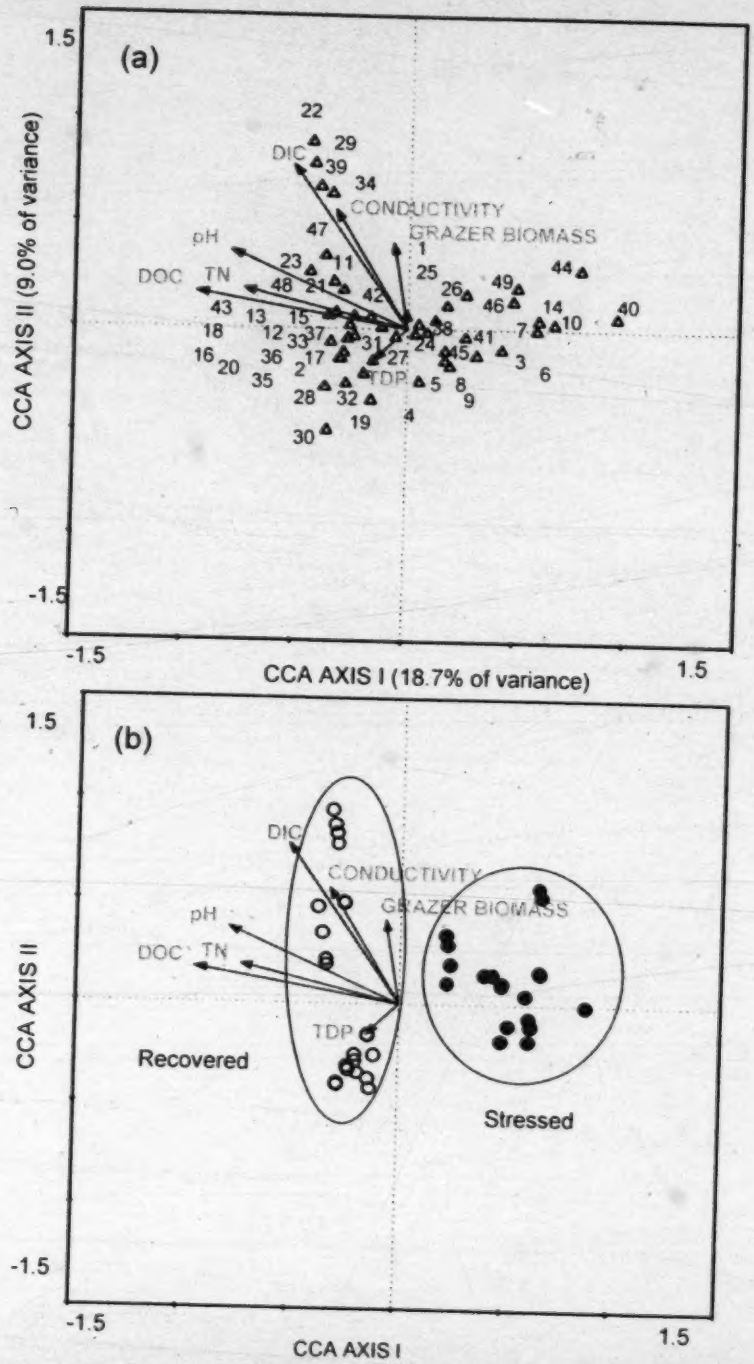

Fig. 3.9. Association of (a) periphyton taxa and (b) lake sampling scores with environmental variables in exclosures in six lakes based on CCA using log_{10}-transformed periphyton biomass, water chemistry (except pH), and grazer biomass data.

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CHAPTER FOUR

GENERAL CONCLUSIONS AND FUTURE RESEARCH

General context

In my thesis, I conducted a survey of benthic communities along a gradient of recovering acidified lakes to develop hypotheses regarding algal-consumer interactions, which were then tested using an exclosure experiment. Contrary to expectations, biotic factors (e.g., grazing) did not replace abiotic regulation (i.e., chemical stress) of periphyton along a lake-recovery gradient. Benthic consumers did alter periphyton species composition, but not its total biomass, which remained significantly suppressed in stressed lakes. The differences between the impacts of consumers and abiotic stress on species composition versus biomass highlighted the capacity of periphyton to compensate functionally for weak, natural (e.g., grazing) disturbances, but not for chronic human stressors (i.e., acidification).

Comparison of survey-based and experimental findings

In general, findings from my exclosure experiment provided support for, and insights into the patterns which I detected for autotrophic and consumer communities during the survey.

Firstly, a nonsignificant relationship between autotrophic and consumer biomass combined with stable isotopic evidence of omnivores relying on

detrital and planktonic carbon sources, suggested weak algal-consumer interactions (Chapter 2). This was weakly supported experimentally as grazing effects could not be detected given the limited power of the study.

Secondly, grazers consistently had a greater influence on autotrophic taxonomic composition than on total biomass considering both survey-based and experimental results. Autotrophic species composition differed between experimental exclosures while total biomass was maintained. As grazer biomass increased, autotrophic community structure was reduced to species with grazer-resistant morphologies (e.g., basal holdfasts, adnate growth form), particularly in recovered lakes. The influence of grazers on the physiognomic structure of autotrophic communities was most pronounced in the chemically recovered lake, providing partial support for the expected replacement of abiotic, with biotic factors as recovery proceeds.

Finally, experimental results confirmed survey-based results showing that autotrophs were suppressed by abiotic stressors rather than consumers. Abiotic factors primarily regulated both autotrophic biomass and species composition. Biomass was significantly greater in less acidic recovered lakes with higher concentrations of dissolved inorganic carbon, owing to an increased abundance of filamentous green algae. Ordination analyses also highlighted the importance of certain abiotic factors (e.g., dissolved organic carbon, pH) as important predictors of autotrophic community composition.

Future research

Future investigations of periphyton communities in recovering acidified lakes would benefit substantially from increased study power. In particular, greater replication is likely needed to detect weak benthic grazing effects on autotrophic communities in unproductive, oligotrophic lakes (e.g., Morin and Cattaneo 1992). Without sufficient replication, future periphyton studies will be prone to committing Type II errors, generating falsely non-significant statistical results.

The persistent importance of abiotic factors to autotrophic and consumer communities suggests that further monitoring of these lakes is required to determine the extent of chemical and biological improvements. Research objectives and monitoring program mandates should be expanded to include watershed catchment characteristics (e.g., soil conditions, resource exploitation) which are potential input sources of stored sulphate. Information on the response time of biotic communities following chemical improvements is need to model biological recovery. While many lakes in the Killarney Park region of central Ontario are showing signs of chemical recovery, some are not and others, still, continue to acidify (Jefferies et al. 2003).

Experimental studies on availability of colonists, dispersal limitations, and colonization success must be implemented at all trophic levels. Sediments could be tested as a viable source of local (i.e., in-lake) colonists, via emergence of dormant cysts or resting eggs. Reciprocal

transplant experiments with local and regional sediments along a water quality gradient could establish if in-lake sources are viable species inoculums or if species pools are regionally depleted. Colonization of a species from a distant source may be necessary, as long-term, regional acidification may have reduced potential immigration from nearby waterbodies (Yan et al. 2003). Empirical studies on the realized potential of aerial dispersal of invertebrates are also required (Bohonak and Jenkins 2003). Following this, synoptic surveys of in-lake colonization success of invertebrates in recovering lakes should be conducted (Snucins 2003). Based on these results, it will become evident which species are able to colonize unassisted and which require human intervention to facilitate recovery.

The prevalence of omnivory and reliance on multiple carbon sources accounted for the weak trophic interaction between benthic consumers and periphyton in our survey. More extensive stable isotope analysis could be done to separate the relative importance of periphyton and detritus as food sources for consumers. Furthermore, the importance of allocthonous sources should be considered as a carbon source, owing to substantial inputs in the littoral area of small boreal lakes (France 1998) and the established flexibility of benthic consumer feeding strategies under stressed conditions (Chapter 2; Dangles 2002). Stable isotope studies could also be used to establish important links between benthic-littoral and pelagic zones in recovering boreal lakes, as alternative carbon

(i.e., energy) sources when resources are limited. Experimental grazing studies should be done to compliment stable isotope studies, to examine edibility of periphyton taxa, focusing on morphological mouthpart limitations of consumers to determine if grazers are forced to adjust their feeding strategies if food availability is limited.

The ecological importance of filamentous green algae (fga) that dominated autotrophic communities of both stressed and recovered lakes warrants further study. Due to inter- and intra-annual variations in biomass (Turner et al. 1995) and infrequent consumption by grazers (Vinebrooke et al. 2001), fga may prove to be an unstable base for the benthic food webs. In addition, due to a tall, erect physiognomy fga may outcompete other periphyton taxa for nutrients and light, restricting colonization success of these species.

To better understand species trophic interactions during recovery, additional food web studies in controlled, mesocosm experiments are needed. For example, the potential compensatory effects of small bodied grazers may have been negated because of increased predation by other acid-tolerant invertebrates, such as odonates and corixids. Therefore, the importance of re-establishing a dominant life form (i.e., fish) on food web structure and interactions in recovering acidified lakes can be tested by in-lake re-introductions using experimental exclosures designs. Studies within large limnocorrals could be used to determine the effectiveness of re-establishing a top consumer on controlling acid-tolerant invertebrate

predators and top down effects on primary consumer and producers. In these studies, densities and type of consumer can be manipulated and controlled.

Final considerations

The establishment of chemical and biological recovery targets in anthropogenically acidified lakes must consider differential species recovery responses and rates, regional differences among ecosystems, and the inevitability of change. Consideration of the impacts of climate change, increased UV-radiation exposure, and trace metal contamination must also be included in assessments of recovery, as the potential interactive effects of these multiple stressors could influence recovery rates and trajectories in acidified lakes. It is possible that benthic community assemblages will not return to pre-stress states because of multiple stressors have changed ecosystems during the recovery period. Certainly, a lack of information on pre-stress communities may restrict our definition of recovery. Instead, recovery progress could be marked as community changes towards those typical of a circumneutral boreal lake. Considering the history and extent of acidification stress in this region, how soon can recovery be expected? Our study provides insight on the relative importance of abiotic and biotic factors in recovering acidified boreal lakes. Future studies are necessary to facilitate recovery, for better management, and restoration of anthropogenically acidified lakes.

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